Patterns of distribution and abundance of larval fish in a southern temperate region

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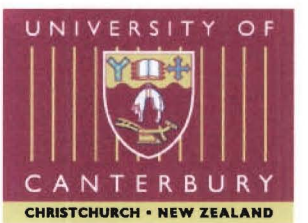

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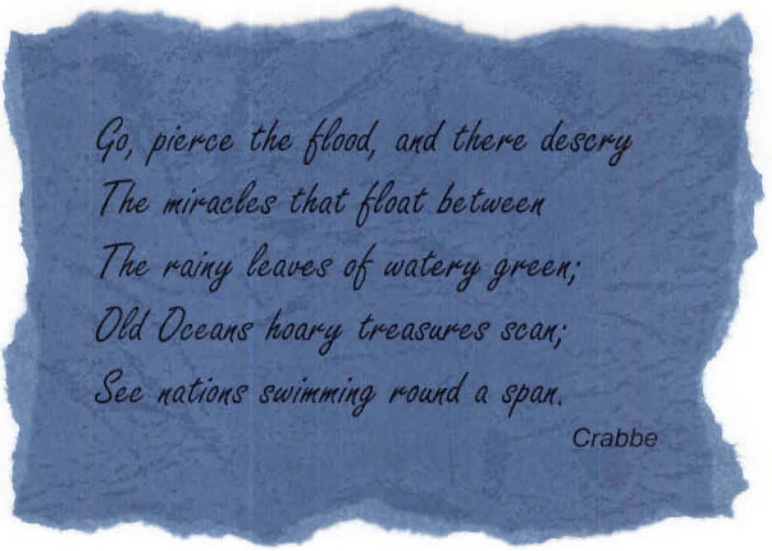

ABSTRACT

The distribution and abundance of larval fish in the Kaikoura region, on the northeastern coast of the South Island of New Zealand, was investigated over a four year period (1994 - 1997). Spatial and temporal variability were described on both broad and fine scales.

Larval fish assemblages at four stations along an offshore transect were sampled fortnightly over an eighteen month period. The abundance and composition of larval fish assemblages were found to vary seasonally. The spawning activity of adults was probably the major determinant of this broad-scale temporal variation in abundance. The timing of spawning activity appeared to be related to the phytoplankton and zooplankton production cycles. The abundance of larval fish at individual offshore stations changed markedly between fortnightly samples. Horizontal movement was considered to be a major cause of this temporal variation.

The timing of peaks in larval abundance was relatively constant between years for most species. However, the annual amplitude of these peaks varied considerably for some species. This annual variability in larval supply is likely to have a major impact on the dynamics of the local fish populations. The temporal abundance patterns of the larval stages of most fish species in the Kaikoura region overlapped broadly with those observed for the same species in northeastern New Zealand.

The abundance of the larval stages of most species varied with distance from shore. Some species were more abundant further from shore and others more abundant near land. However, there was little evidence to support the generalisation that larvae that are more abundant nearshore hatch from demersal eggs, whereas those that are more widely distributed are derived from pelagic eggs

The alongshore distribution of larvae was investigated at four stations at increasing distances from rocky reefs. Although the larval stages of many species were dispersed at least 6 km offshore, some larval fish, including several that were abundant offshore, appeared to resist alongshore dispersal. These species probably use a combination of active swimming, schooling behaviour and eddies to prevent alongshore dispersal.

The fine-scale vertical distribution of larval fish in surface waters was investigated over 24 hr periods. The abundance of the larval stages of most species varied within a 24 hr period. Diel vertical migration was considered to be the major cause of this variation. For some species, the degree of vertical migration appeared to depend on ambient light levels.

The horizontal distribution of larval fish in inshore surface waters was strongly influenced by the presence of surface slicks. Larval fish were considerably more abundant within surface slicks than in the surface waters either side of them. This aggregation, together with the shoreward movement of slicks, suggests that surface slicks may transport larval fish towards shore.

A new design of light trap was tested in inshore waters. These traps successfully attracted and captured larval fish in inshore habitats. Although the light traps caught a subset of the species taken by plankton nets, they were equally capable of detecting seasonal and lunar phase differences in larval fish abundance.

The conclusion of this study was that although local oceanographic processes can directly influence the broad-scale distribution of larval fish, these distributions can be modified markedly by fine-scale processes and the behaviour of larval fish. The ability of the larval stages of many species of fish to adjust their horizontal and vertical position and to maintain a station in suitable habitats results in distributions that are both structured and complex.

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Chapter One

General Introduction

1.1 INTRODUCTION

Ichthyoplankton is a generic term used to describe the eggs and larval stages of fish in the pelagic environment. However, just as many components of the plankton are not completely without locomotory ability, larval fish are not passive particles at the mercy of local currents (Leis & Goldman 1984). The larval stages of many species are competent swimmers that can change their vertical position, swim at surprisingly high speeds and swim in a highly directional way (Leis *et al.* 1996). Consequently, neither the distribution nor abundance of fish larvae in the pelagic environment is random. This thesis is concerned with the ecology of fish during their larval phase.

The early life history of most teleost fish includes a pelagic, usually larval, phase (Leis 1991a). Most species spawn externally in the water column and the fertilised eggs may subsequently undergo oceanic advection and diffusion. Even in species that produce demersal eggs or are viviparous, newly hatched larvae usually enter the pelagic environment. In most cases, the pelagic stages of fish differ markedly from adults of the same species in their morphology, habitat preference, food requirements and behaviour. During the pelagic phase, mortality of eggs and larvae is extremely high and only a tiny proportion of fish survive (Houde 1987).

At the end of their planktonic phase, which may last from days to months (Brothers & Thresher 1985, Victor 1986, Wellington & Victor 1989), the surviving larvae of demersal or reef-associated fish settle as juveniles onto reefs or into associated inshore environments where they mature and may eventually enter local adult populations. For species that have a pelagic adult phase, metamorphosis to a juvenile stage represents the end of the planktonic phase (Kendall *et al.* 1984). The bipartite nature of the life history of most fish species has important implications for their biology and for attempts to understand that biology.

Research in the area of the early life history of fish has been diverse (see reviews by Saville & Schnack 1981, Alderdice 1985, Doherty & Williams 1988, Leis 1991a), but most studies can be grouped into three broad categories according to their primary objectives (Heath 1992):

1. Determination of the abundance of exploited populations.
2. Determination of the processes that produce recruitment variability.
3. Understanding ecosystem and marine population dynamics.

1.2 ASSESSMENT OF EXPLOITABLE POPULATIONS

Some of the first studies on fish eggs and larval stages were attempts to understand and predict the spawning times and distributions of major exploited fish species. Classic publications of this nature include McIntosh (1890), Masterman (1892), Holt (1893) and Kyle (1897). The concept of assessing the abundance of a fish population from the numbers of eggs or larvae in the plankton originated towards the end of the 19th century. The basic concept was simple: the annual production of eggs from a population equals the product of the abundance of mature females in that population and the mean annual fecundity of those females.

The first egg survey for stock assessment purposes was carried out in the North Sea in 1895 to determine the spawning biomass of plaice (Hensen & Apstein 1897). This pioneering

attempt was based on many assumptions concerning the biology and distribution of plaice and attracted much criticism (Murray & Hjort 1912). However, egg and larval surveys have since become an important part of the stock assessment procedure in many areas of the world despite continuing problems with interpretation of the data.

Northern anchovy, *Engraulis mordax*, off the coast of southwest California have been the focus of the longest running and best developed egg surveys for biomass estimation (Picquelle & Hewitt 1983, Bindman 1986). However, while egg production surveys are appropriate for species that spawn pelagic eggs, they are not suitable for those species that deposit demersal eggs. While techniques exist for egg surveys of species that spawn demersal eggs inshore (Dempsey & Bamber 1983, Clarke & King 1985), they are of little use for species like Atlantic herring, *Clupea harengus*, that deposit demersal eggs at a large number of widely spaced, imprecisely known locations (Haegele & Schweigert 1985). In these instances, larval surveys are often employed to obtain a relative index of spawning biomass.

Larval surveys are based on the concept that the average abundance of larvae over the spawning season is proportional to the spawning biomass. As with egg surveys, a number of assumptions are necessary to support this relationship. In particular, the reproductive output of adults, the survival of eggs and the growth and mortality rates of larvae are all assumed to be constant from year to year and to be independent of initial stock biomass. Annual surveys of larval herring for estimating spawning stock biomass have been widely used in the north Atlantic. In the North Sea, larval surveys began in 1940's and have continued ever since (Saville 1971). These surveys are primarily used to assess year-class abundance.

Knowledge of recruitment levels to exploited fish stocks, defined as year-class abundance, is essential for management of fisheries. Estimates of current levels of recruitment can be obtained from surveys or fisheries directed at the recruits, but forecasts must be based on surveys of pre-recruitment abundance (i.e., larval or early juvenile stages). The main assumption in predicting recruitment levels from surveys of pre-recruits is that mortality rates are constant from year to year over the period between the survey and recruitment. While surveys earlier in the life history are more valuable for management purposes, the assumption of consistent mortality becomes more difficult to justify as the period between survey and recruitment increases.

Most early attempts at relating larval abundance to subsequent recruitment levels were not successful (e.g., Rae 1953), primarily because these studies were based on very few sampling years. However, more recently the abundance of larval Arctic cod, *Boreogadus saida*, has been found to be correlated with juvenile abundance (Sundby *et al.* 1989) and the abundance of larval Baltic herring, *Clupea harengus harengus*, was correlated with subsequent recruitment levels (Parmanne & Sjoblom 1987). Even with the assistance of larval abundance surveys, recruitment variability remains the single least understood problem in fishery science (Houde 1987).

1.3 PROCESSES AFFECTING RECRUITMENT

Early fisheries scientists (e.g., Fabre-Domerque & Biétrix 1897, Hjort 1914) identified that variations in adult biomass were caused by irregular fluctuations in recruitment that were unrelated to spawning effort. These variations are established during the early life history stages of fish and are thereafter preserved in the age structure of the population. Hjort (1914) proposed two major hypotheses to explain the control exerted on adult population size by events during the pelagic phase. The first of these was that larval survival is dependent on critical food densities at the time of yolk-sac exhaustion. However, subsequent research has failed to demonstrate a universal dependence on the first feeding stage as the most important life history event for marine fish (Heath 1992).

Hjort's "critical period" hypothesis was elaborated by Cushing (1975) in his hypothesis that year-class strength was determined by the match or mismatch of spawning and seasonal production cycles. However, while this hypothesis seems valid in many instances (Sherman *et al.* 1981, Townsend 1984, Jenkins 1986, Haldorson *et al.* 1993), there are examples of species that have poor recruitment during seasonal plankton blooms (Iles & Sinclair 1982, Sinclair *et al.* 1985) and of species that flourish in regions without seasonal production cycles (Sinclair & Tremblay 1984). The importance of food availability was further emphasised by Lasker (1975), who hypothesised that localised concentrations of prey organisms enhance the survival of larval fish. Events that destabilise and disperse these prey patches (e.g., wind and storms) may be a major cause of interannual variability in recruitment (Lasker 1981, Wroblewski 1984, Peterman & Bradford 1987, Wroblewski & Richman 1987).

While Hjort's critical period hypothesis is still held in esteem, it has become increasingly clear that recruitment variability results from factors other than unfavourable drift away from nursery grounds or starvation once the yolk-sac is exhausted (Houde 1987). A large number of experimental, field and theoretical studies have pointed to high and variable mortality during the early life history of fish as the cause of often vast differences in year-class abundances (Houde 1987, Pepin 1991). The agents of this mortality are predation, starvation or dietary deficiency and oceanographic conditions that advect ichthyoplankton into unsuitable environments (Houde 1987).

Predation plays a dominant role in larval mortality (Hunter 1981, Lasker 1981, Hunter 1984, Sissenwine 1984), although it may vary depending on species and developmental stage (Theilacker 1986). The pelagic stages of fish are consumed by a wide variety of predators including pelagic cnidarians and ctenophores (Purcell 1981, 1984, 1985, 1989, Purcell & Grover 1990), chaetognaths (Pearre 1976, Hunter 1981, 1984, Fortier & Harris 1989), other larval fishes (Jenkins *et al.* 1984, Young & Davis 1990, Finucane *et al.* 1991), adult reef fish (Hobson & Chess 1978, Hamner *et al.* 1988, Tsukamoto *et al.* 1989), coastal pelagic fish (Colin 1976) and pelagic fish (Reintjes & King 1953, Dragovich 1970, Daan *et al.* 1985, Hopkins 1989). Any change in the exposure of larval stages to this predation through variability in the temporal or spatial abundance of predators is likely to alter mortality rates and produce recruitment variability.

Predation in larval fish is related to body size and not age (Purcell *et al.* 1987, Bailey & Houde 1989). Startle and escape responses in larval fish increase with size and eventually render attacks by most invertebrates unsuccessful (Bailey & Yen 1983, Bailey 1984, Yen 1987). Therefore, unfavourable growth conditions, not necessarily those leading to starvation, that prolong stage durations can substantially increase the period of vulnerability to predation in larval fish (Hunter 1981, Houde 1987, Pepin 1991). Even modest changes in daily growth rates can cause major changes in mortality rates, and thus recruitment levels, if they occur during the larval stage when growth rates are highest and initial numbers in the cohort are also large (Houde 1987).

Reduced growth rates can affect larval mortality by restricting the size of prey that can be captured and processed. Progressive starvation can decrease the searching and feeding abilities of larval fish (Richards & Lindeman 1987). Many studies have shown that the maximum and range of sizes of prey items in the diet of larval fish increase with size (Hunter 1981, Nishiyama & Hirano 1985, Heath 1989). Consequently, larvae that have restricted growth may face starvation though lack of access to suitably sized prey (Hunter 1981). Even small changes in life stage durations due to reduced prey-concentration, prey-quality or both can lead to large increases in mortality (Houde 1987).

Practically every important organismal-level biological factor influencing the survival of ichthyoplankton is affected by interrelated dynamic oceanographic and meteorological processes (Richards & Lindeman 1987). The vital rates affecting survival (mortality rates, growth rates, stage durations) and energetics of larval fish are all strongly affected by temperature (Houde 1989, 1994, Morse 1989). Temperature and body size are likely to be the main variables affecting egg and larval stage dynamics (Pepin 1991) and prey consumption rates (Mackenzie *et al.* 1990). Consequently, several studies have found that year-class strength is linked to temperature variability between years (Mysak *et al.* 1982, Murray *et al.* 1983, Swartzman *et al.* 1983, Hansen & Buch 1986, Planque & Fox 1998).

Strong interactions exist between sea surface temperatures, winds and currents (Heath 1985). These interactions mean that dynamic meteorological processes often result in dynamic oceanographic processes. The resulting cessation of, or variability in, advective processes has direct implications for larval survival.

Hjort (1914) also hypothesised that larval survival is determined by advection which may prevent larvae from finding suitable pelagic environments during their planktonic phase or fail to transport larvae to suitable nursery grounds at the end of their larval period. A variety of physical processes can generate recruitment variability by influencing the dispersal or retention of larval fish (Leis & Miller 1976, Nelson *et al.* 1977, Bailey 1981, Parrish *et al.* 1981, Iles & Sinclair 1982, Longhurst 1984, Norcross & Shaw 1984, Sinclair & Tremblay 1984, Sinclair *et al.* 1985, Lobel & Robinson 1986). These processes include: geostrophic and wind influenced current regimes (wind-induced mixing of the surface layer, Langmuir circulations and upwelling); discontinuities in temperature, salinity and nutrients associated with frontal zones of gyres, eddies or coastal plumes; tidal forces; shallow water internal waves; and bottom boundary-layer dynamics (Richards & Lindeman 1987).

The dispersal of larval fish, particularly larval reef fish, during their planktonic phase is considered to offer an adaptive advantage. This advantage may result from the avoidance of predators (Johannes 1978), from energy saved by not swimming against tidal currents (Bourret *et al.* 1979), from enabling recolonisation of patchy environments (Barlow 1981) or by allowing the propagules to spread widely over a pelagic environment that offers only patchy survival (Doherty *et al.* 1985). Many aspects of spawning behaviour have been interpreted as mechanisms to maximise the flushing of eggs and larvae away from reefs or spawning areas (Johannes 1978, Ross 1983, Doherty 1983a, Thresher 1984, Hunt von Herbing & Hunte 1991). The failure of advective processes to facilitate dispersal could result in increased mortality.

While larvae found offshore may require oceanic conditions to complete their pelagic phase, their dispersal could also be an accidental, even detrimental, consequence of their reproductive mode and hatchling morphology, especially for pelagic spawners (Brogan 1994a). Retention in specific areas (e.g., near reefs) may be beneficial to some species in terms of increased availability of food and reduced expatriation (Brogan 1994a). Larval fish that are not retained in these areas may experience increased mortality.

1.4 ECOSYSTEM AND POPULATION DYNAMICS

If the structure and persistence of fish populations are strongly influenced by processes acting during the planktonic stages, during settlement or immediately after settlement (Williams 1980, Sale *et al.* 1985) and adult population size is determined during the pelagic stage (Doherty 1983b), then the answers to questions regarding recruitment variability and population dynamics lie in understanding the pelagic phase (Doherty & Williams 1988). There is a growing consensus that the population dynamics of fishes are largely controlled by the delivery of competent larvae to settlement sites (Doherty & Williams 1988, Underwood & Fairweather 1989, Doherty 1991, Sale 1991, Milicich *et al.* 1992, Meekan *et al.* 1993, Milicich & Doherty 1994) and that larval replenishment may exert long-term influences over the abundance and demography of adult populations. There is little doubt that knowledge of larval biology is crucial to an understanding of the population dynamics of fish species. However, the ecology of larval fish cannot be fully understood without an understanding of the physical oceanography, chemical oceanography and biological oceanography of a study area (Smith & Lasker 1978). This information is necessary to understand the positioning of larval fish in the pelagic ecosystem and thus to understand fish population dynamics.

Before the processes influencing the survivorship of larval fish and recruitment variation can be understood, descriptive information on the distribution of ichthyoplankton needs to be gathered (Kingsford 1986). An understanding of where larvae spend their time away from the adult populations is integral to all other studies of the pelagic stage (Leis 1991a). This is especially true in areas such as New Zealand where the ichthyoplankton is only partially known.

1.5 ICHTHYOPLANKTON STUDIES IN NEW ZEALAND

The vast majority of studies on larval fish in New Zealand have been done on the northeastern coast of the North Island (see review by Kingsford 1988). These studies have

focussed on seasonality (Thompson 1983, Kingsford 1986, Roper 1986), vertical distribution patterns (Kingsford 1986, Kingsford & Choat 1986, Kingsford & Milicich 1987), horizontal distributions (Crossland 1980, Crossland 1981, Crossland 1982, Kingsford 1986, Cole 1987, Kingsford & Choat 1989, Tricklebank *et al.* 1992), age and growth (Kingsford 1980, Park 1984, Milicich 1986, Atkinson 1987, Kingsford & Milicich 1987) and onshore transport (Kingsford 1986, Kingsford & Choat 1986).

In southern New Zealand, ichthyoplankton research has been based predominantly around the Otago Peninsula. Most early studies were purely descriptive (Anderton 1906, Graham 1939, Graham 1956), but more recent studies (Robertson & Raj 1971, Robertson 1973, 1975a, 1975b, 1976, 1978, 1980, 1981, McDowall & Robertson 1975, Robertson *et al.* 1978, Robertson & Mito 1979) have increased the knowledge of larval fish and eggs in southern New Zealand.

The surface waters along the Kaikoura coast are nutrient-rich and highly productive, providing breeding and feeding grounds for large numbers of fish, sea birds and marine mammals. Several studies have investigated ichthyoplankton assemblages hundreds of kilometres off the Kaikoura coast over the Chatham rise (Robertson 1976, 1978, Robertson *et al.* 1978, Robertson & Mito 1979), but only one study has sampled larval fish in the nearshore environment. During her study of primary- and zooplankton production in the Kaikoura region, Grieve (1966) often encountered larval fish but did not attempt to identify them.

1.6 RATIONALE FOR THIS THESIS

The objective of this thesis was to investigate the ecology of larval fish in the pelagic environment around the Kaikoura Peninsula. To do this, it was important to recognize that the pelagic environment is not physically structureless and uniform, but is instead highly structured, complex and heterogeneous both horizontally and vertically (Bakun 1986, Hamner & Wolanski 1988, Wolanski & Hamner 1988). Consequently, the distribution of fish larvae is also highly structured in all dimensions (Leis 1991a). Therefore, any study of the ecology of larval fish must include both horizontal and vertical components.

To obtain information on the ecology of larval fish, it is important to investigate both broad and small scale distribution patterns. Broad scale distribution patterns are important, but small scale patterns may be the source of the often considerable variation observed in large scale studies (Fasham 1978, Haury *et al.* 1978, Fortier & Leggett 1984, Leis 1991a, Williams & English 1992, Lennert-Cody & Franks 1999). In order to identify and rank sources of variation, a range of scales needs to be included in a sampling design.

This thesis is comprised of a set of mensurative experiments with designs capable of identifying important sources of variation in the broad and small scale spatial and temporal distribution patterns of larval fish. The thesis contains five results chapters (Chapters 3-7). The first three results chapters investigate the offshore, alongshore and vertical distribution patterns, respectively, of fish larvae in coastal and shelf waters around the Kaikoura Peninsula. The fourth results chapter is a methodological investigation comparing the performance of two gear types for sampling larval fish. The last results chapter is an investigation of the effect of small scale

hydrological processes on the distribution and abundance of larval fish. The main questions that were examined in each chapter are given below.

Chapter 3. What are the effects of distance offshore and time (both short term (fortnight) and long term (1 yr)) on the distribution and abundance of larval fish in the Kaikoura region? This chapter describes the seasonal changes in distribution, abundance, size, composition and richness of ichthyoplankton at stations off the Kaikoura coast and examines the overlap between fish species and zooplankton abundance both in space and in time.

Chapter 4. Can reef fish larvae resist alongshore dispersal on an exposed coast? This chapter investigates larval retention in reef-based species and whether it is related to the type of eggs (pelagic vs demersal) that each species releases. The extent of the alongshore and vertical distribution of fish larvae in the near-shore environment is described. Retention is also related to the offshore distribution patterns observed in Chapter 3.

Chapter 5. Do larval fish in the nearshore environment have a stratified vertical distribution? This chapter examines diel changes in the vertical distribution of larval fishes in coastal waters. Distribution patterns are described at various times of the day and night during two phases of the moon. Seasonal effects are also investigated.

Chapter 6. Can light traps be used to sample larval fish in temperate regions? This chapter compares the sampling characteristics of a light trap and a plankton net. The investigation concentrates on whether the two sampling methods yield the same taxonomic composition, relative abundance of taxa and size frequency of fish larvae. The two sampling methods are used to describe the distribution and abundance of larval fish in two inshore habitats during two seasons and two moon phases.

Chapter 7. Is the distribution and abundance of larval fish affected by surface slicks? This chapter investigates the effect of surface slicks on larval fish in the nearshore environment. The investigation concentrates on the movement of slicks and examines the distribution of ichthyoplankton in and out of slicks.

Appendix 1 is a reprint of Hickford & Schiel (1999) which was published from material presented in Chapter 6.

Chapter Two

General Methods

2.1 INTRODUCTION

This chapter describes the physical features and hydrology of the study region, as well as the general methods of sampling, sorting and identification of ichthyoplankton and data analysis that are used throughout this thesis. More specific methods sections are included in each chapter.

2.2 STUDY AREA

Fish larvae were sampled in coastal and shelf waters around the Kaikoura Peninsula from 1994-1997 (Fig. 2.1). Projecting approximately four kilometres out from the Marlborough coast, the Kaikoura Peninsula is the smallest of three large peninsulas along the South Island's east coast.

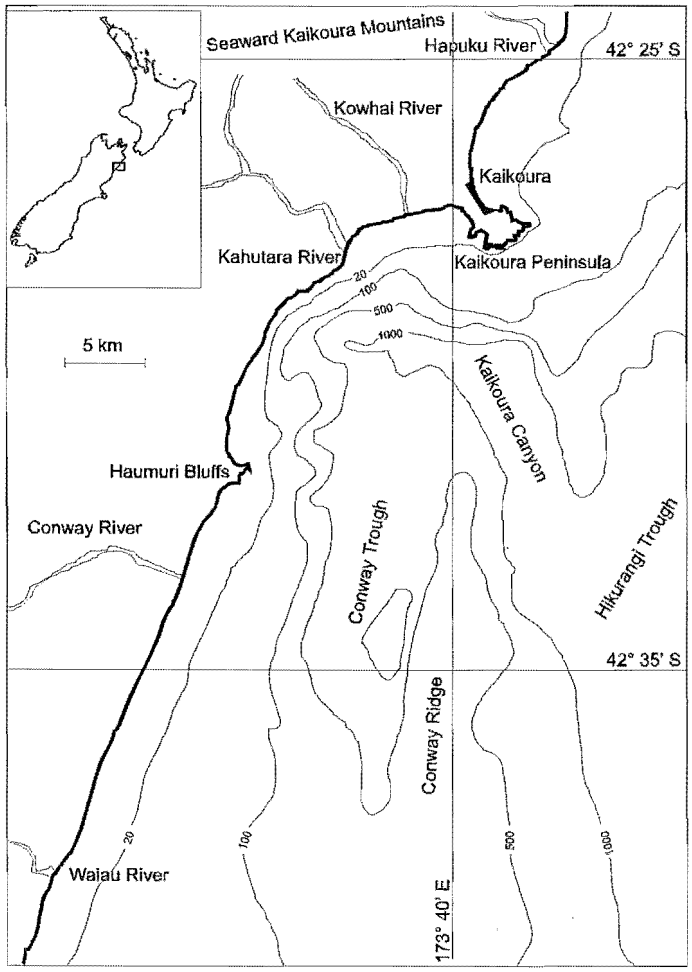

Figure 2.1. Map of the study area showing the Kaikoura Peninsula and coast. Bathymetry is in metres.

The Kaikoura Peninsula was formed by the uplifting of a "limestone island" in the Late Pleistocene and Early Holocene (Chandra 1969). Platforms of white, grey and pink argillaceous limestone (Amuri limestone) and argillaceous siltstone dominate the southeast face of the Peninsula. The northeast and southeast faces are dominated by nodular flinty limestone overlain by Amuri limestone, glauconitic and argillaceous siltstone (Chandra 1969). The coastal plains to the north and south of the Peninsula are composed of alluvial deposits from the Seaward Kaikoura range, which rises to over 2500 m within 16 km of the coast. Several rivers

flow from the Seaward Kaikoura range: the Hapuku river north of the Peninsula, and the Kowhai, Kahutara and Conway Rivers to the south (Fig. 2.1). The very steep longitudinal profile of these rivers and other smaller streams in the region (Chandra 1969) produce frequent flooding and heavy sediment loads. Further to the south, the Waiau River drains water from the Southern Alps.

The continental shelf off the Kaikoura coast is demarcated by the southern reach of the Hikurangi Trough (Fig. 2.2). The Kaikoura Canyon extends westward from the southern end of the Hikurangi Trough, with depths of 1000 m within 4 km of the coast south of the Peninsula. The Conway Trough extends southwards from the canyon and is separated from the Hikurangi Trough by the Conway Ridge, which rises to depths of just over 110 m.

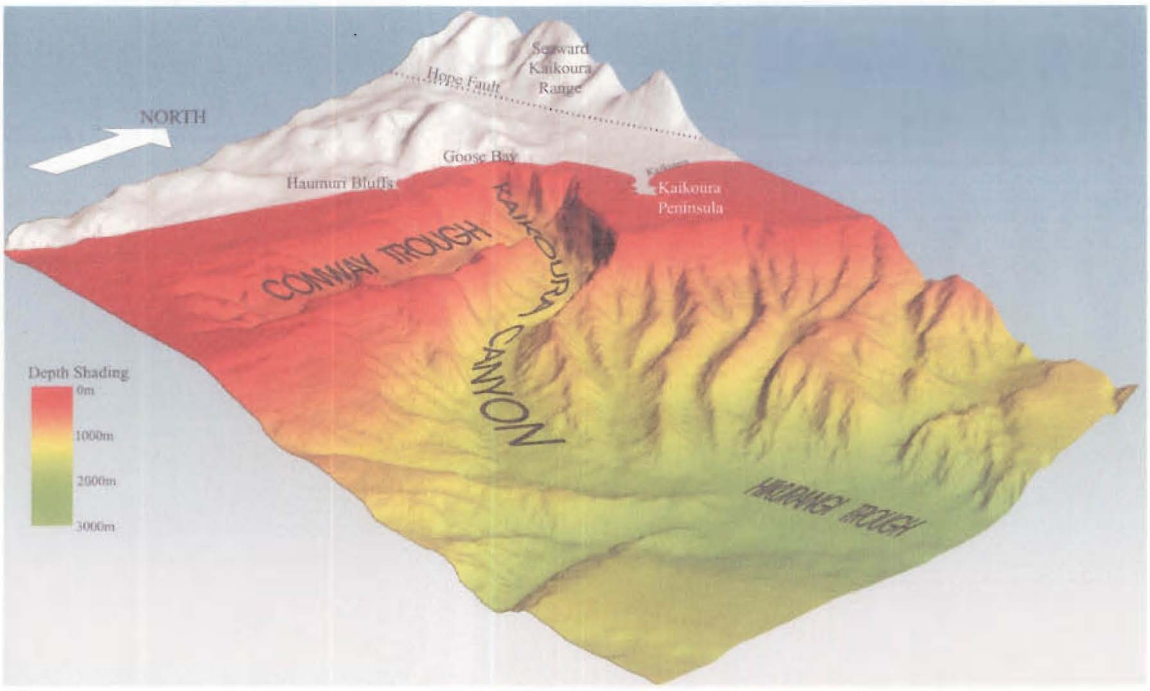

Figure 2.2. Oblique terrain model of the Kaikoura Canyon and surrounding area. The model has been illuminated from the east and the vertical scale has been exaggerated five times (from Lewis *et al.* 1998).

The sediments of the Hikurangi Trough and Kaikoura Canyon are predominately mud. However, the immediate subtidal zone and the continental shelf around the Peninsula are covered by fine sand, pebble gravel, boulders and rocky reef (Lewis *et al.* 1998).

The Kaikoura coast is exposed to frequent southerly storm events in winter. On most days in spring, summer and autumn, onshore northeasterly winds develop and intensify in the afternoon. The limestone composition of the Peninsula, together with the outflow from local rivers and wave action, often results in a distinct murky inshore band of water.

The coastal and shelf waters off the Kaikoura region support a wide variety of fish species that in turn support a diverse commercial fishery. The shallow reefs and kelp stands along the coast sustain large populations of reef fish species (Hickford & Schiel 1995). The nutrient-rich coastal waters also support a wide range of pelagic species. The narrowness of the continental shelf means that deep-water oceanic species are often found close to shore.

2.3 LOCAL HYDROLOGY

The hydrology of the Kaikoura coast is dominated by two features: the Kaikoura Canyon and the subtropical convergence. During winter, the Canyon allows the intrusion close to shore of warm water that is moving southwards in the Hikurangi Trough (Garner 1953, Houtman 1965). Coastal mixing and river outflows produce upwelling of this nutrient-rich subtropical water during the winter months (Garner 1961). The Kaikoura Peninsula also represents the northern limit of the subtropical convergence. South of Kaikoura, the warm, saline, subtropical water of the East Cape Current meets the cooler, less saline subantarctic water of the Southland Current in the Southland Front (Heath 1972c). In summer, the convergence of these two water masses produces upwellings of cold, nutrient-rich subsurface waters against the shelf (Garner 1961).

The dominant current in the Kaikoura region is the northward-moving Southland Current. One component of this current turns offshore near Kaikoura, but the other extends as far north as 40° S close inshore, after sweeping across the southern end of Cook Strait around Cape Campbell (Heath 1985). Few data are available on fine-scale nearshore hydrology in the Kaikoura region.

2.4 SAMPLING TECHNIQUES

Two methods were used for sampling ichthyoplankton during this study: plankton nets and light traps. Two different plankton nets were used. The main net was a box-pyramid design, with a 0.5 m^2 mouth (Fig. 2.3).

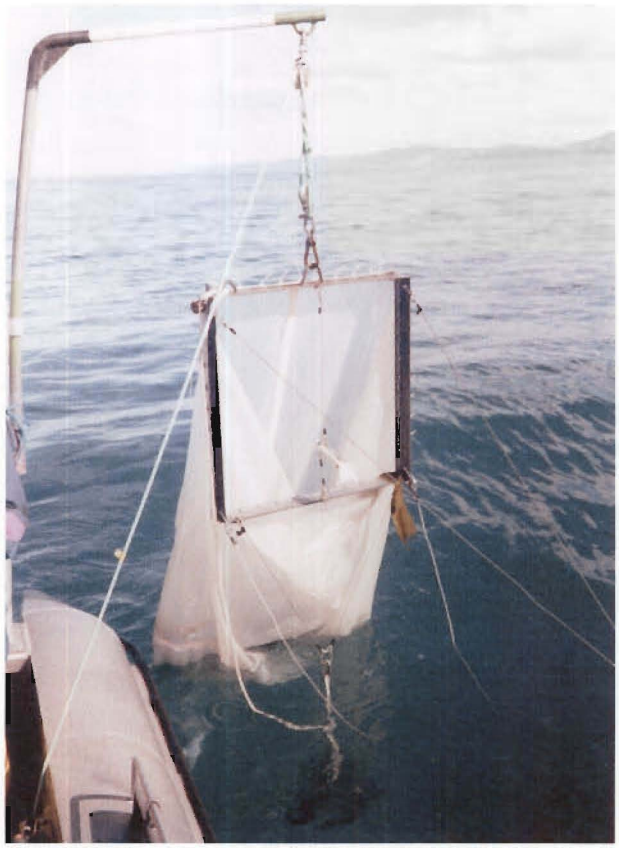

Figure 2.3. The 0.5 m^2 plankton net being lifted from the water. The Scripps depressor (submerged) is suspended from the lower edge of the frame.

The net was designed to sample large volumes of water. To prevent clogging when plankton densities were high, it was constructed with a mesh area that was 11 times that of the mouth area (Fig. 2.4). The net was constructed from 280 µm nybolt mesh, and all seams were sealed with reinforcing tape.

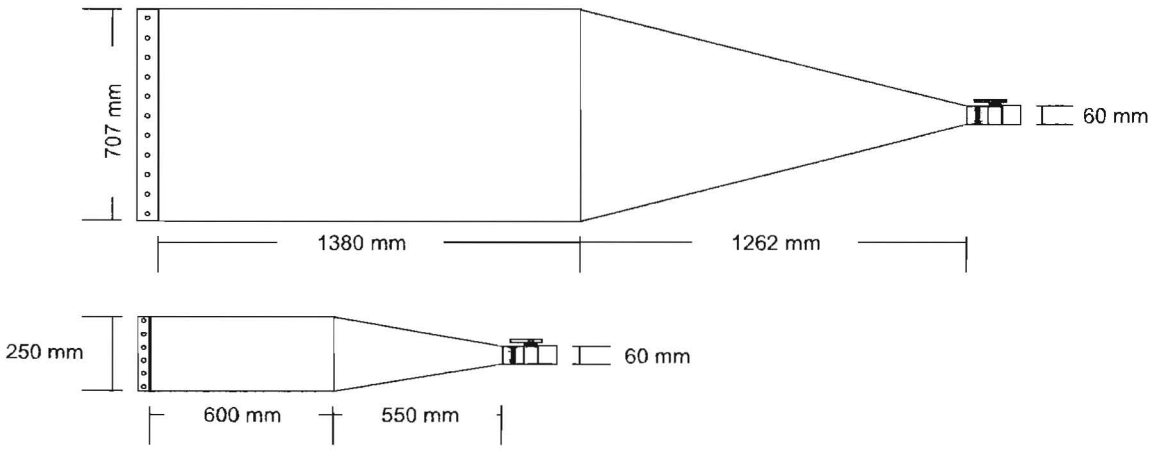

Figure 2.4. Diagram of the 0.5 m^2 plankton net (upper) and the 0.0625 m^2 plankton net (lower). The mouth area: mesh area ratio is 1:11 for the large net and 1:14 for the smaller net.

A large-bore PVC gate-valve was attached to the cod end of the plankton net (Fig. 2.5). The valve was closed during tows, but could be opened to release the sample at the completion of a tow. The interior of the valve was very smooth and allowed the sample to flow easily out of the cod end.

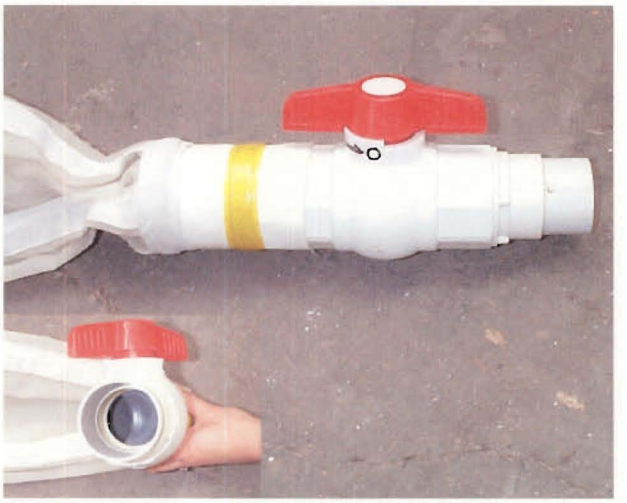

Figure 2.5. The cod end of the 0.5 m^2 plankton net. The gate-valve provides a secure seal during tows and a simple means of emptying the net when open (it is partially opened in the insert).

The gate-valve was modified to allow the attachment of plastic sample tubes (48 mm diameter) (Fig. 2.6). The junction between the gate-valve and the sample tube (Fig. 2.6) was fitted with mesh windows (250 µm stainless steel) to allow samples to drain to a fixed volume (2 L). At the completion of a tow, a sample tube was attached to the end of the net and the gate-valve was opened, allowing the sample to enter the tube. Pumped seawater was used to wash the net thoroughly.

Figure 2.6. The sample tubes. The tubes were pre-loaded with buffered formalin, and were attached to the cod end of the net at the completion of a tow with the mesh-walled connector (insert).

The plankton net was towed beside the Tawaki, a 6 m Stabicraft boat (Fig. 2.7). Heavily reinforced towing arms were fitted to the bow of the boat so that the net could be towed alongside, avoiding any disturbance from the boat's wake. Counterweights (two large plastic drums with holes drilled in their bases) were towed off the opposite arm to allow the boat to maintain a straight track (Fig. 2.7).

Figure 2.7. The Tawaki configured for surface tows with the 0.5 m^2 plankton net. Note the towing arms fitted to the bow, and the counterweights (orange and blue drums) being towed on the opposite side of the boat from the net.

A gantry with an extendable arm was attached to the stern of the boat. The top of the net's frame was suspended from this arm by a pulley system (Fig. 2.3). The pulley system allowed the net height in the water column to be adjusted and fixed. A 25 kg Scripps depressor was suspended from the lower edge of the net frame to keep the net mouth vertical in the

water column (Fig. 2.3). The net was towed with a four-point bridle that joined above the mouth of the net to avoid disturbance caused by the wire strops (Fig. 2.8). A large spring (from the mechanism of a garage door) was used to attach the tow wires to the arms at the bow of the boat. This spring dramatically reduced the pressure on the arms from any surface chop during surface tows, and allowed the net to track more smoothly.

Figure 2.8. The 0.5 m^2 plankton net being towed at the surface. The uppermost edge of the frame is suspended 10 cm above the surface. Note the four-point bridle joining above the mouth of the net.

For surface tows, the uppermost edge of the net frame was fixed at 10 cm above the water surface (the flowmeter was submerged at all times) (Fig. 2.8). For deeper tows (1 m and 3 m), different bridles (with increasingly shorter upper strops) were attached to the net, which was lowered using the pulley system until the uppermost edge of the frame was at the appropriate depth. At the completion of a tow, the boat was stopped before the net was raised using the pulley system (Fig. 2.3).

A second smaller plankton net was used for tows within surface slicks (Fig. 2.4). This net had a 0.0625 m^2 mouth, and was constructed from 280 µm nybolt mesh. It was also a box-pyramid design, but it had a mouth area: mesh area ratio of 1:14. The top of the net frame was attached to a reinforced pole that could be lowered beside the boat so that the uppermost edge of the net was fixed at a depth of 0.5 m. This net also had a gate-valve mechanism attached to the cod end to allow samples to be transferred to the sample tubes.

When samples contained large numbers of salps (*Ihlea magahanica*, *Salpa thompsoni*, *Iasis zonaria* and *Thalia democratica*), *Munida gregaria* or large amounts of drift algae, they

were filtered through a 8 mm mesh sieve prior to being fixed. This process removed the bulk of the salps, *Munida* or drift algae. Any fish that were large enough to be caught in the sieve were easily seen and collected.

The volume of water filtered by the plankton nets was measured with a General Oceanics flowmeter (Model 2030R). This was mounted within the mouth of the net, positioned at 0.33 of the net width (Fig. 2.3). Towing speeds were monitored using a hull-mounted speedometer (Humminbird Wide-eye), and were checked with readings from the flowmeter. A towing speed of between 1.2 ms^{-1} and 1.5 ms^{-1} was maintained on most occasions. The accuracy of the flowmeter was checked regularly by towing the net over a fixed distance.

The light traps used in this study were a modified version of the design described by Doherty (1987). The body of the light trap was made from a 240 L mobile plastic waste bin (Sulo, Australia), divided by two opaque partitions into three chambers (Fig. 2.9). Three sides of the upper chamber were fitted with clear plastic windows (290 x 190 mm), each containing two moulded entrance slots. Each horizontal slot tapered from 60 x 300 mm down to 12 x 250 mm. The partitions separating the chambers contained two identical slots. The middle chamber had no external entrance slots, but was fitted with a 250 x 300 mm clear plastic window. The lower chamber was fitted with 0.5 mm stainless steel mesh panels (240 x 150 mm) on three sides, and a 50 mm drain hole (closed with a rubber stopper). The light traps were suspended below an anchored buoy so that the entrance slots into the light trap were 1.5 m below the surface.

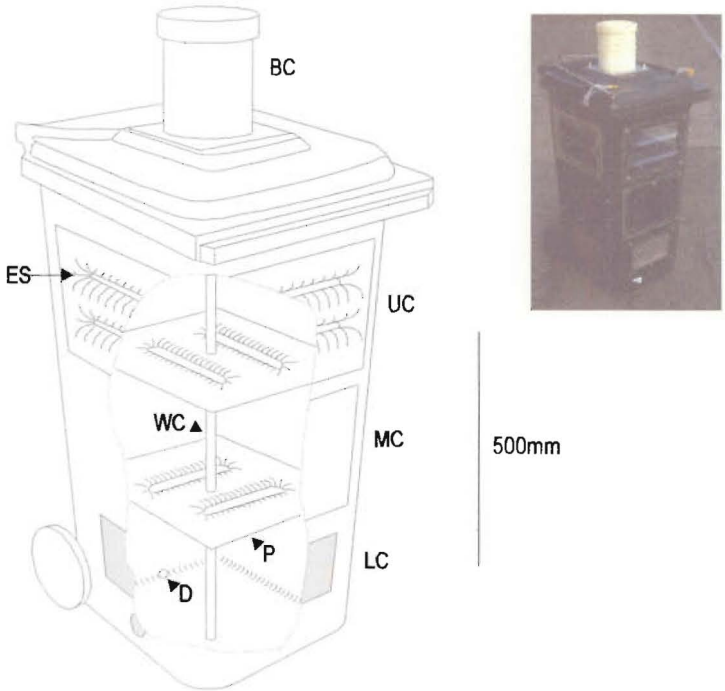

Figure 2.9. Diagram of a light trap (pictured in insert) with the side partially removed. BC: battery chamber; UC: upper chamber; MC: middle chamber; LC: lower chamber; P: partition; D: drain; WC: waterproof core; ES: entrance slot.

A central waterproof core ran through all three chambers. The upper section of the core was constructed from 150 mm wastepipe, and contained a rechargeable lead-acid battery (12 v 10 Ah) and a digital timing mechanism. The lower section of the core was constructed from 40 mm clear plastic, and contained the three light sources (6 W fluorescent tubes). Each of the light sources was contained solely within a chamber. The timer mechanism was identical to that described by Doherty (1987), with the light in the lower chamber remaining lit throughout the sampling sequence and the lights in the upper and middle chambers alternating at 5 min intervals.

At the completion of a sample, the light traps were lifted onto the boat using the gantry and pulley system, and washed thoroughly with pumped seawater. The mesh panels in the lower chamber of the light trap allowed all but 1.72 L of water to drain from the trap. This water, which contained the sample, was then drained into a bucket by releasing the rubber stopper.

2.5 PRESERVATION AND IDENTIFICATION

The sample tubes for transferring plankton from the plankton nets and buckets from the light traps were pre-loaded with formalin (200 ml) and sodium borate buffer (80 ml) so that when mixed, the sample was immediately fixed in buffered 10% formalin in seawater. In the laboratory, the samples were drained and transferred to fresh 5% formalin in seawater and stored in plastic bottles. At a later date, all fish larvae were removed from the samples using a dissecting microscope (10x ocular, 1x objective) and the method described by Smith & Richardson (1977). All larvae were identified to the lowest possible taxonomic level, counted and stored in buffered 2% formalin in freshwater. In most instances, all larvae (except those that were badly damaged) were measured to the nearest 0.5 mm by placing them on a graduated slide. Notochord length was measured for preflexion and flexion larvae, and standard length was measured for postflexion larvae.

All fish larvae were named according to Paulin *et al.* (1989). Only *Tripterygion capito* (Paulin *et al.* 1989) has been re-described in a new genus, and is now *Grahamina capito* (Fricke & Roberts 1993). The identification of fish larvae was achieved using descriptions and illustrations from Baker (1972), Crossland (1981, 1982), Dolphin (1997), McDowall (1990), Moser *et al.* (1984), Neira *et al.* (1998), Robertson (1976), Robertson & Mito (1979) and Ruck (1971, 1973a, 1973b, 1980). In addition to these published descriptions and illustrations, a reference collection that was compiled throughout the study helped considerably with identification.

Seventeen species previously undescribed as larvae, pre-juveniles or pelagic juveniles in New Zealand waters were collected and identified (by fin ray counts and size series) during this study. These were described and illustrated by Dolphin (1997), and include *Stokellia anisodon*, *Diaphus* sp., *Pseudophycis bachus*, *Echiodon pegasus*, *Paratrachichthys trailli*, *Leptonotus elevatus*, *Helicolenus barathri*, *Scorpaena papillosus*, *Congiopodus coriaceus*, *Lepidoperca* sp., *Taumakoides rua*, *Mendosoma lineatum*, *Grahamina capito*, *Grahamina signata*, *Gobiopsis atrata*, *Seriolella caerulea* and *Colistium guntheri*. A full list of the fish larvae collected and identified in this study is given in Table 2.1.

Table 2.1. Summary of the 79 taxa from 41 families found during this study. Samples also contained larvae from 20 unknown taxa.

Family	Taxon	Family	Taxon
Clupeidae	*Sprattus* spp.	Tripterygiidae	Unidentified Tripterygiids
Gonorynchidae	*Gonorynchus gonorynchus*		*Bellapiscis medius*
Retropinnidae	Unidentified Retropinnids		*Forsterygion spp.*
	Stokellia anisodon		*Forsterygion lapillum*
Galaxiidae	Unidentified Galaxiids		*Forsterygion varium*
Sternoptychidae	*Maurolicus muelleri*		*Gilloblennius tripennis*
Photichthyidae	*Vinciguerria attenuata*		*Grahamina capito*
Myctophidae	*Benthosema suborbitale*		*Grahamina signata*
	Diaphus spp.		*Notoclinus fenestratus*
	Gymnoscopelus piabilis		*Ruanoho decemdigitatus*
	Lampanyctodes hectoris	Clinidae	*Cologrammus flavescens*
	Symbolophorus boops		*Cristiceps aurantiacus*
Moridae	Unidentified Morids	Eleotrididae	*Grahamichthys radiata*
	Auchenoceros punctatus	Gobiidae	*Gobiopsis atrata*
	Pseudophycis bachus	Gempylidae	*Thyrsites atun*
Gadidae	*Gaidropsarus novaezelandiae*	Istiophoridae	*Hyperoglyphe antarctica*
Merlucciidae	*Macruronus novaezelandiae*	Centrolophidae	*Seriolella* spp.
Carapidae	*Echiodon pegasus*		*Seriolella brama*
Gobiesocidae	*Diplocrepis puniceus*		*Seriolella caerulea*
	Gastroscyphus hectoris	Bothidae	*Arnoglossus scapha*
	Trachelochismus melobesia		*Lophonectes gallus*
	Trachelochismus pinnulatus	Pleuronectidae	*Colistium guntheri*
Hemiramphidae	*Hyporhamphus ihi*		*Pelotretis flavilatus*
Scomberesocidae	*Scomberesox saurus*		*Peltorhamphus* spp.
Trachichthyidae	*Paratrachichthys trailli*		*Peltorhamphus latus*
Syngnathidae	*Hippocampus abdominalis*		*Peltorhamphus novaezeelandiae*
	Leptonotus elevatus		*Rhombosolea plebeia*
	Leptonotus norae		*Rhombosolea retiaria*
	Lissocampus filum	Monacanthidae	*Parika scaber*
Scorpaenidae	Unidentified Scorpaenids	Unknown	Unknown 1
	Helicolenus barathri		Unknown 2
	Scorpaena papillosus		Unknown 3
Congiopodidae	*Congiopodus coriaceus*		Unknown 4
	Congiopodus leucopaecilus		Unknown 5
Triglidae	*Chelidonichthys kumu*		Unknown 6
Serranidae	*Lepidoperca* spp.		Unknown 7
Acanthoclinidae	*Acanthoclinus fuscus*		Unknown 8
	Taumakoides rua		Unknown 9
Carangidae	*Trachurus declivis*		Unknown 10
Latrididae	*Mendosoma lineatum*		Unknown 11
Mugilidae	*Aldrichetta forsteri*		Unknown 12
Labridae	*Notolabrus* spp.		Unknown 13
	Notolabrus celidotus		Unknown 14
Odacidae	*Odax pullus*		Unknown 15
Bovichthyidae	*Bovichtus variegatus*		Unknown 16
Uranoscopidae	*Genyagnus monopterygius*		Unknown 17
Creediidae	Unidentified Creediid		Unknown 18
	Limnichthys rendahli		Unknown 19
Leptoscopidae	*Crapatalus novaezealandiae*		Unknown 20
Percophidae	*Hemerocoetes monopterygius*		

2.6 STATISTICAL ANALYSIS

Two main types of data were collected during this study. The ichthyoplankton samples contained a wide range of taxa, allowing tests on the abundance of individual taxa and species richness. Because most undamaged fish larvae were also measured, the size of larvae could be compared among samples.

All data manipulation and collation was done using Microsoft Excel (95, 97 & 2000). StatSoft Statistica 5.1 was used for statistical analysis, and graphical presentation was done using Microsoft Excel, GraphPad Prism 2.01 and CorelDraw 8.

Prior to any statistical analysis, the counts of fish larvae from each sample were standardised. Using the volume of water filtered by the plankton net, the counts were adjusted to numbers per standard volume (usually 500 m^3). The volume of water sampled by the light traps was not known and, therefore, counts could not be standardised or readily compared to plankton net samples.

The designs of most of the individual studies lent themselves to multifactorial analysis of variance (ANOVA). Prior to any ANOVA, the raw data were tested for homogeneity of variance using Cochran's test. Most count data required a log (x + 1) transformation to become homogeneous. In the few cases where the data did not respond to transformation and the variances remained heterogeneous, ANOVA was continued with caution. ANOVA is robust and operates well even under considerable heterogeneity of variances as long as sample sizes are approximately equal (Glass *et al.* 1972). After ANOVA, the variance was often partitioned (Winer 1962) to estimate the proportion of variation accounted for by each factor in the ANOVA model. Tukey's Honest Significant Difference tests were used for *post hoc* comparison of means.

Correlation analysis was used to identify taxa with similar abundance patterns. When dealing with count data, the raw data were log (x + 1) transformed prior to analysis. The resulting correlation matrices were corrected for multiple comparisons by using an adjusted α level (Ezekiel 1945). The corrected α level was derived from the equation

$$\alpha_{corrected} = \frac{0.05}{no.of\ correlations}$$

This correction reduces the chance of a Type I error when making multiple comparisons. When significant correlations were observed, Principal Components Analysis was used to identify groupings of taxa and samples. PCA was done using Canoco and Canopost. Count data were log (x + 1) transformed prior to PCA.

Chapter Three

Offshore Distribution Patterns of Larval Fish

3.1 INTRODUCTION

It is generally accepted that the probability of survival of fish eggs and larvae through their planktonic phase is enhanced by them being in a favourable habitat (Frank & Leggett 1983). Such a habitat is defined by a combination of physico-chemical factors (salinity (Peterson *et al.* 1999), temperature (Malloy & Targett 1991) and circulation patterns (Frank & Leggett 1983)) and biological factors such as the abundance of prey and predators (Ware 1975, Leggett & Deblois 1994). In temperate regions, many of these factors follow seasonal patterns, with changes in water temperature and circulation inducing changes in primary production and in turn the abundance of potential prey and predators of larval fish (Cushing 1975). A fish species that maximises the probability of survival by spawning at a time that places offspring in a good habitat should have a selective advantage. Many studies, therefore, have shown that fish larvae in temperate regions are not randomly distributed in time or space (Roper 1986, Tricklebank *et al.* 1992). Instead, larvae are typically produced in large numbers at specific times, and are often concentrated in discrete patches both horizontally and vertically.

The horizontal distribution of ichthyoplankton in coastal waters can be influenced by proximity to reefs (Kingsford & Choat 1989), linear oceanographic features (Kingsford *et al.* 1991), cross-shelf advective processes (Smith *et al.* 1999) and eddies (Lobel & Robinson 1986). The horizontal distribution of fish larvae can also be influenced by biological factors. Many researchers have related the horizontal distribution of ichthyoplankton to egg type, with larvae hatched from demersal eggs being found closer to shore than those from pelagic eggs (Leis & Miller 1976, Marliave 1986, Kingsford & Choat 1989, Suthers & Frank 1991, Brogan 1994a). Many authors have also found distinct differences between nearshore and offshore ichthyoplankton assemblages (Young *et al.* 1986, Sabatés & Masó 1990, Gray 1993).

Although information concerning the horizontal and temporal distribution of ichthyoplankton abounds for a wide range of coastal and shelf areas around the world, relatively few studies have been done in New Zealand. Most of these New Zealand studies have been concentrated off the Northland coast (see review by Kingsford 1988) including several on seasonality (Thompson 1983, Kingsford 1986, Roper 1986, Tricklebank *et al.* 1992) and horizontal distribution (Kingsford & Choat 1989, Tricklebank *et al.* 1992). However, little attention has been given either to the horizontal or temporal distribution of larval fish in the cooler waters around the South Island.

The hydrological situation in the Kaikoura region is known to be complex (Garner 1953), but most meso-scale coastal processes have not been described. Fluctuating subtropical (oceanic) influences and varying discharges from rivers in the region cause coastal characteristics to fluctuate. The bottom configuration, in conjunction with current and wind systems, produces upwellings of nutrient-rich cold water into the warmer surface waters in summer (Garner 1961, Heath 1972a) and upwellings of warm water into the colder surface waters in winter (Houtman 1965). The Kaikoura phytoplankton has a conspicuous bloom in spring, and zooplankton numbers (particularly copepods) increase and peak during this period (Grieve 1966).

The aim of this study was to test the effects of distance offshore and time (both short term (approx 2 wk) and long term (1 yr)) on the distribution and abundance of larval fish in the Kaikoura region. This chapter describes the seasonal changes in distribution, abundance, species composition and species richness of the ichthyoneuston, and examines differences in life history strategies of the abundant larvae and the overlap among different species in both space and time.

3.2 METHODS

3.2.1 Study area

Sampling was done at four stations along a transect that extended 6 km due south from the south side of the Kaikoura Peninsula (Fig. 3.1). The first station was 50 m offshore (42° 29.750' S; 173° 40.886' E), at a water depth of 12 m and within South Bay. South Bay is surrounded by rocky reefs, but is very exposed to southerly storms. The second station was 2 km offshore (42° 26.837' S; 173° 40.819' E), at a water depth of 56 m. The third station was 4 km offshore (42° 27.921' S; 173° 40.883' E), at a water depth of 83 m. The final station was 6 km offshore (42° 29.001' S; 173° 40.809' E), at a water depth of approximately 850 m.

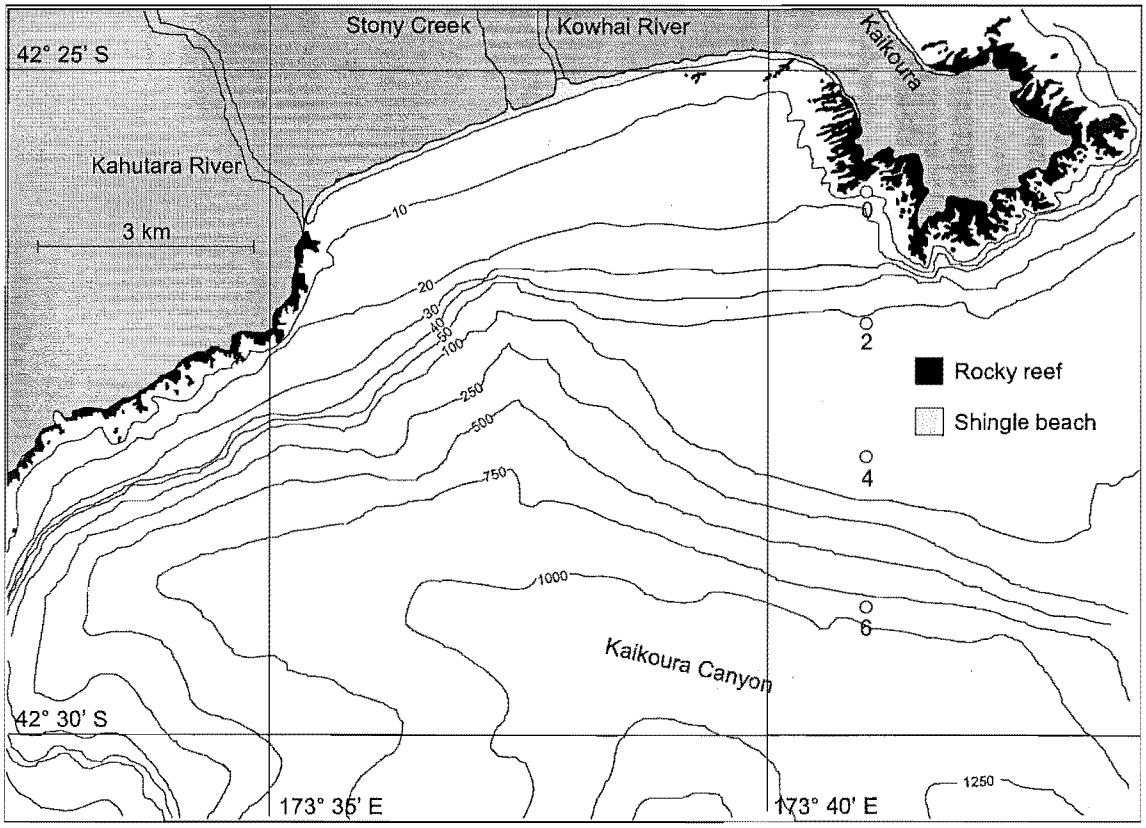

Figure 3.1. Map of the Kaikoura Peninsula on the northeast coast of the South Island. The four offshore stations (0, 2, 4 and 6) are shown. Bathymetry is in metres.

3.2.2 Sampling procedure

Ichthyoplankton surveys were done fortnightly between October 1995 and May 1997. Sampling was completed during daylight hours in the early morning. Logistical constraints required that stations were always sampled in the same order, i.e. working towards shore.

Neustonic ichthyoplankton was sampled using a plankton net with a 707 x 707 mm mouth (0.5 m^2) and 280 µm mesh. The net was a box-pyramid design with a filtration efficiency of 1:11. A General Oceanics flowmeter (Model 2030R) was fitted within the mouth of the net (positioned at 0.33 of the net width) to determine the volume of water filtered per tow. The net was rigged to be towed alongside a 6 m boat to avoid disturbance caused by the wake. The top of the net's frame was suspended from a gantry so that it sampled with the uppermost edge of the net at a fixed height of 10 cm above the sea surface. A 25 kg Scripps depressor was suspended from the lower edge of the frame to keep the net's mouth vertical in the water column. The net was towed with a four-point bridle that joined above the waterline to avoid disturbance caused by the wire strops. Three 15 min tows, at a speed of ca. 1.3 ms^{-1}, were made at each station. The net filtered an average of 500 m^3 of water per replicate.

After the completion of each sample, the plankton net was washed thoroughly with pumped seawater and the sample was fixed in buffered 10% formalin in seawater. All fish larvae were removed from the samples using a dissection microscope, identified to the lowest possible taxonomic level, counted and stored in buffered 2% formalin in freshwater. Counts were standardised to the number of fish per 500 m^3. Clupeid, retropinnid and galaxiid larvae could not be identified beyond the family or genus level because of the similarities of larvae from individual species and the presence of adults from several species of each of these families in the study area. Small scorpaenids, labrids, tripterygiids, centrolophids and pleuronectids could also not be identified below the family or genus level. All fish (except those that were badly damaged) were measured to the nearest 0.5 mm by placing them on a graduated slide. Notochord length was measured for preflexion and flexion larvae, and standard length was measured for postflexion larvae.

Prior to each plankton tow being made, the surface water temperature was measured using an electronic thermometer (Humminbird Wide-eye) fixed to the hull of the boat. Hourly wind speed and direction measurements for the period immediately prior to each sampling occasion were obtained from the Kaikoura Automatic Weather Station (G23464) situated on top of the Kaikoura Peninsula (42° 25.020' S; 173° 40.980' E).

3.2.3 Analysis

Two types of data were collected during this study. The ichthyoplankton samples contained a wide range of taxa, allowing tests on both the temporal and spatial distribution of individual taxa and species richness. Because all undamaged fish larvae were measured, the size of larvae could also be compared spatially and temporally.

Two-factor ANOVAs, with time (up to 37 occasions) and distance from shore (4 stations) as factors, were used to compare the abundance of commonly occurring taxa (> 0.3% of the total number caught), all taxa combined and species richness. The number of occasions that were compared in the ANOVA varied between taxa because any occasion when no larvae (of the taxon of interest) were collected were excluded from the analysis. Prior to ANOVA, the data for each taxon were tested for homogeneity of variances using Cochran's test and all data

became homogeneous when log (x+1) transformed. Tukey's Honest Significant Difference (HSD) tests were used for *post hoc* comparison of means.

ANOVA was used to compare the size of larvae from each commonly occurring taxon caught at each station. Tukey Honest Significant Difference (HSD) tests were used for *post hoc* comparison of means. Temporal variability could not be formally tested because larvae from even the most common taxa were not caught on all, or even most, occasions.

Correlation analysis of mean monthly abundance was used to investigate any similarities in the temporal distribution of commonly occurring taxa. The resulting correlation matrices were corrected for multiple comparisons by using an adjusted α level (Ezekiel 1945). The corrected α level was derived from the equation

$$\alpha_{corrected} = \frac{0.05}{no.\ of\ correlations}$$

Principal components analysis (PCA) of mean monthly abundance was then used to display the relationship between time and the taxonomic composition of the samples. Data were log (x+1) transformed prior to analysis.

3.3 RESULTS

3.3.1 Ichthyoplankton abundance

In total, the 444 samples collected 28,638 larval and pelagic juvenile fish from 31 families (Table 3.1). Fifty-eight taxa were identified, including eight that contained more than one species (identifiable to the family or genus level) and three unidentified taxa. The damaged category contained larvae that were unidentifiable as a result of the damage they sustained during capture. The three most abundant taxa accounted for 64% of the total catch. They were Unidentified tripterygiids (22.17%), *Grahamina capito* (21.80%) and Unidentified scorpaenids (20.04%). All but fourteen taxa comprised less than 0.2% of the total number of larvae collected. Of these fourteen more common taxa, only *Bovichtus variegatus* occurred in less than 10% of the samples. Instead of occurring in very low numbers throughout the sampling period, most of the less numerous taxa occurred in only a few samples. Eight taxa occurred only in the three replicates taken at a single station (< 0.7% occurrence) and thirteen occurred only in a single tow (0.2% occurrence).

Overall, 26,243 larval fish (92% of all larvae collected) were measured. The sizes of these ranged from a 1 mm *G. capito* to a 73 mm *Hippocampus abdominalis*. Within the most common taxa, the mean larval size ranged from 2.2 mm for unidentified scorpaenids to 25.5 mm for retropinnids. The overall mean size of larval fish captured was 8.2 mm.

There was considerable variation among the common taxa both in the habitat occupied by their adults and in their mode of spawning (Table 3.2). Many of the common taxa hatched from demersal eggs, but viviparous taxa and larvae from pelagic eggs were also common. Most of the common taxa had adults who occupied rocky reef habitats, but pelagic, anadramous (retropinnids) and amphidromous taxa (galaxiids) were also common.

Table 3.1. Composition and size range of fish larvae in the samples. Total abundance (n), percentage of total catch when adjusted for volume (%), percentage occurrence in the 444 samples (% Occ), the number measured and their mean, minimum and maximum size (mm) are given for each taxon.

Family	Taxon	n	%	% Occ	Measured	Mean	Min	Max
Clupeidae	*Sprattus* spp.	213	0.77	17.1	202	16.3	5	34
Retropinnidae	Retropinnidae	1168	4.64	22.7	1160	25.5	6.5	43.5
Galaxiidae	Galaxiidae	400	1.60	25.9	380	20.6	5	46
Sternoptychidae	*Maurolicus muelleri*	2	0.01	0.5	1	8.5	8.5	8.5
Photichthyidae	*Vinciguerria attenuata*	1	0.004	0.2	1	46.0	46	46
Myctophidae	*Benthosema suborbitale*	1	0.004	0.2	1	22.5	22.5	22.5
	Gymnoscopelus piabilis	187	0.62	10.1	172	13.0	5.5	40
Moridae	*Auchenoceros punctatus*	28	0.10	6.1	27	16.7	5	37
	Pseudophycis bachus	12	0.05	1.8	11	34.7	23	55
Gadidae	*Gaidropsarus novaezelandiae*	26	0.09	3.8	26	26.4	7	55
Merlucciidae	*Macruronus novaezelandiae*	5	0.02	1.1	5	8.4	4	17
Carapidae	*Echiodon pegasus*	7	0.03	0.9	7	11.2	6.5	31
Gobiesocidae	*Gastroscyphus hectoris*	1	0.003	0.2	1	5.0	5	5
	Trachelochismus melobesia	8	0.03	0.9	8	6.1	4	14
Hemirhamphidae	*Hyporhamphus ihi*	10	0.04	1.8	10	7.5	3.5	12
Scomberesocidae	*Scomberesox saurus*	3	0.01	0.5	3	16.5	6.5	25
Syngnathidae	*Hippocampus abdominalis*	28	0.10	5.2	27	24.7	12.5	73
	Leptonotus elevatus	4	0.01	0.9	4	19.1	17	22
Scorpaenidae	Unidentified Scorpaenidae	5379	20.04	33.1	5334	2.2	1.5	10
	Helicolenus barathri	23	0.10	2.3	23	11.7	5.5	14
	Scorpaena papillosus	1	0.004	0.2	1	16.5	16.5	16.5
Congiopodidae	*Congiopodus leucopaecilus*	2	0.01	0.5	2	5.5	5.5	5.5
Triglidae	*Chelidonichthys kumu*	10	0.03	1.8	8	8.8	3	14
Acanthoclinidae	*Acanthoclinus fuscus*	1	0.004	0.2	1	3.0	3	3
	Taumakoides rua	3	0.01	0.5	3	3.7	3.5	4
Mugilidae	*Aldrichetta forsteri*	493	1.81	15.3	461	12.7	3	49
Labridae	*Notolabrus* spp.	14	0.05	1.4	14	12.0	7.5	15.5
	Notolabrus celidotus	5	0.02	0.9	5	9.3	8.5	10
Bovichthyidae	*Bovichtus variegatus*	139	0.47	9.5	139	6.4	4	31
Uranoscopidae	*Genyagnus monopterygius*	1	0.004	0.2	1	19.5	19.5	19.5
Tripterygiidae	Unidentified Tripterygiidae	6614	22.17	42.6	5073	7.5	2.5	19
	Forsterygion spp.	2002	7.21	12.2	1908	6.3	4	20.5
	Forsterygion lapillum	17	0.06	2.0	17	11.9	6	17.5
	Forsterygion varium	2187	7.33	27.3	2128	12.6	4.5	34
	Gilloblennius tripennis	2190	7.16	24.1	2146	10.2	3.5	18.5
	Grahamina capito	6436	21.80	35.6	6068	7.7	3	23
	Grahamina signata	3	0.01	0.5	3	5.3	5	6
	Ruanoho decemdigitatus	689	2.40	26.4	653	6.4	3	25.5
	Notoclinus fenestratus	10	0.04	1.8	9	4.7	4	6
Eleotrididae	*Grahamichthys radiata*	1	0.003	0.2	1	5.0	5	5
Gobiidae	*Gobiopsis atrata*	2	0.01	0.5	2	3.0	2.5	3.5
Gempylidae	*Thyrsites atun*	7	0.02	1.6	7	23.1	12	55
Istiophoridae	*Hyperoglyphe antarctica*	1	0.004	0.2	1	36.0	36	36
Centrolophidae	*Seriolella* spp.	14	0.06	2.5	14	6.2	3	9.5
	Seriolella brama	5	0.02	0.7	5	9.9	4	17
	Seriolella caerulea	3	0.01	0.7	3	30.8	24.5	40
Bothidae	*Arnoglossus scapha*	10	0.03	1.8	9	14.4	3	26
	Lophonectes gallus	2	0.01	0.5	2	9.3	7.5	11
Pleuronectidae	*Pelotretis flavilatus*	1	0.004	0.2	1	6.0	6	6
	Peltorhamphus spp.	1	0.003	0.2	0	-	-	-
	Peltorhamphus novaezelandiae	3	0.01	0.5	3	7.8	7.5	8
	Peltorhamphus latus	1	0.003	0.2	2	7.8	6	9.5
	Rhombosolea plebeia	97	0.34	11.7	96	6.1	2	17
	Rhombosolea retiaria	1	0.003	0.2	1	7.0	7	7
Monacanthidae	*Parika scaber*	36	0.14	3.8	35	16.2	7	28
	Unknown 3	2	0.01	0.5	2	3.3	3	3.5
	Unknown 12	3	0.01	0.5	3	5.0	4	7
	Unknown 20	1	0.003	0.2	1	7.5	7.5	7.5
	Damaged	124	0.44	13.1	12	8.0	5	13.5
Total		28638			26243	8.2	1.5	73

Table 3.2. Life history characteristics of the fourteen common taxa collected in the samples. The habitat occupied by adult fish and their mode of spawning are indicated. Habitats: IP, inshore pelagic; F, freshwater & estuaries; R, rocky reef; S, sand. Mode of spawning: P, pelagic eggs; FD, freshwater demersal eggs then marine larvae; D, demersal eggs; V, viviparous; ?, unknown.

Family	Taxon	Adult	Spawning	Source
Clupeidae	*Sprattus* spp.	IP	P	Ayling & Cox 1987
Retropinnidae	Retropinnidae	IP,F	FD	McDowall 1990
Galaxiidae	Galaxiidae	F	FD	McDowall 1990
Myctophidae	*Gymnoscopelus piabilis*	P	?	Robertson *et al.* 1978
Scorpaenidae	Scorpaenidae	R	P,V	Ayling & Cox 1987
Mugilidae	*Aldrichetta forsteri*	IP, F	P	McDowall 1990
Bovichthyidae	*Bovichtus variegatus*	R	?	Robertson & Mito 1979
Tripterygiidae	Unidentified Tripterygiidae	R	D	Crossland 1981
	Forsterygion spp.	R	D	Crossland 1981
	Forsterygion varium	R	D	Crossland 1981
	Gilloblennius tripennis	R	D	Crossland 1981
	Grahamina capito	R	D	Crossland 1981
	Ruanoho decemdigitatus	R	D	Crossland 1981
Pleuronectidae	*Rhombosolea plebeia*	S, F	P	Ayling & Cox 1987

The abundance of the common taxa at the four stations was highly variable through time (Table 3.3). However, all taxa had significant interactions between time and distance offshore, which accounted for a large proportion of the variance in the model. On most occasions, the nearshore (0 km) and offshore (2 km, 4 km and 6 km) abundances of all of the common taxa (except retropinnids and *G. capito*) were not significantly different (Table 3.4). However, for most of the common taxa any differences in abundance, where they did occur, were consistent. For example, the number of *G. capito* larvae did not differ between the nearshore and offshore sites on 11 of the 23 occasions in which they were found. However, on each of the remaining 12 occasions, significantly less *G. capito* larvae (Tukey HSD, $p < 0.05$) were caught at the nearshore station (0 km) than at one or more of the offshore stations (Table 3.4).

Table 3.3. Summary results from ANOVA of the abundance of fourteen common taxa and all taxa combined with time (up to 37 occasions) and distance offshore (0 km, 2 km, 4 km and 6 km) as factors. The variance has been partitioned (%) for each factor and the interaction term. Significance is indicated (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$).

Taxon	Time			Distance			Interaction			Residual	
	df	F	%	df	F	%	df	F	%	df	%
All taxa	36	41.6***	55	3	10.3***	1	108	8.5***	33	296	11
Taxonomic richness	36	35.3***	62	3	1.9	0	108	4.3***	23	296	15
Sprattus spp.	22	8.4***	34	3	7.6***	4	66	2.4***	29	184	33
Retropinnidae	20	13.7***	17	3	215.9***	41	60	8.2***	31	168	11
Galaxiidae	24	11.5***	34	3	26.2***	10	72	3.5***	31	200	25
Gymnoscopelus piabilis	10	8.0***	19	3	23.0***	16	30	6.4***	45	88	21
Unidentified Scorpaenidae	23	47.9***	60	3	25.7***	4	69	6.8***	26	192	10
Aldrichetta forsteri	16	24.1***	55	3	6.5***	3	48	3.2***	22	136	20
Bovichtus variegatus	7	5.3***	21	3	7.4***	13	21	2.4**	30	64	37
Unidentified Tripterygiidae	31	37.9***	52	3	18.6***	3	93	8.1***	34	256	11
Forsterygion spp.	9	39.9***	64	3	3.2*	2	27	4.2***	20	80	14
Forsterygion varium	26	70.2***	57	3	56.0***	5	78	12.9***	31	216	7
Gilloblennius tripennis	22	35.2***	55	3	11.0***	2	66	6.5***	30	184	13
Grahamina capito	22	63.5***	51	3	42.0***	5	66	15.3***	37	184	7
Ruanoho decemdigitatus	26	25.7***	48	3	1.3	0	78	6.6***	37	216	15
Rhombosolea plebeia	21	3.4***	14	3	22.5***	13	63	3.1***	39	176	34

Table 3.4. Results of Tukey HSD tests on mean abundance of fourteen common taxa at nearshore (0 km) and offshore (2 km, 4 km, 6 km) stations. The total number of occasions when each taxon was found (Total), the number of occasions when there were more larvae found at the nearshore station than at one or more of the offshore stations (More)(Tukey HSD, $p < 0.05$), when there was no significant difference (NS) and when less larvae were found nearshore (Less) are shown.

Taxon	Total	More	NS	Less
All taxa	37	9	17	11
Species Richness	37	4	30	3
Sprattus spp.	23	0	21	2
Retropinnidae	21	11	10	0
Galaxiidae	25	0	21	4
Gymnoscopelus piabilis	11	0	8	3
Unidentified Scorpaenidae	24	3	20	1
Aldrichetta forsteri	17	0	15	2
Bovichtus variegatus	8	0	7	1
Unidentified Tripterygiidae	32	1	25	6
Forsterygion spp.	10	0	8	2
Forsterygion varium	27	2	17	8
Gilloblennius tripennis	23	1	19	3
Grahamina capito	23	0	11	12
Ruanoho decemdigitatus	27	2	20	5
Rhombosolea plebeia	22	4	18	0

The total number of larvae from all taxa varied both temporally and spatially (Table 3.3). The peak abundance of fish was found during late May (Fig. 3.2), but numbers of larvae also were high during October and January. This pattern parallels the peaks in abundance of the three dominant taxa: unidentified tripterygiids during May and unidentified scorpaenids and *G. capito* during January.

The taxonomic richness of the samples also varied both temporally and spatially (Table 3.3). There were no general patterns in the number of taxa either across time or with distance offshore (Fig. 3.2), The highest peaks tended to occur during summer, but this was not consistent. Overall, therefore, numbers varied but species richness did not with distance offshore.

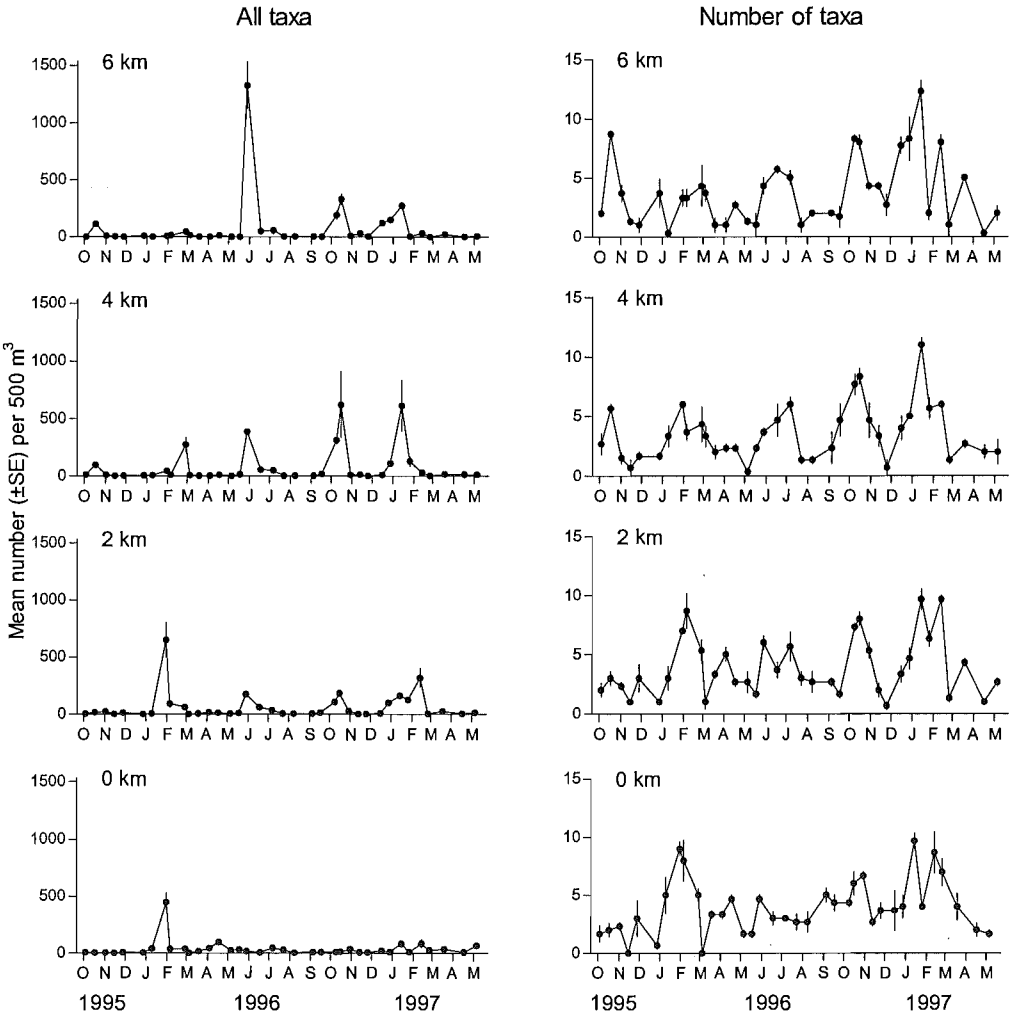

Figure 3.2. Mean number per 500 m^3 of all taxa and taxonomic richness at the four stations between October 1995 and May 1997.

When the data were pooled across all occasions, the greatest number of larvae from all taxa combined occurred at 4 and 6 km from shore, with relatively few larvae at 0 km and 2 km (Fig. 3.3). The pooled abundance of the fourteen common taxa at each of the four stations showed a range of patterns (Fig. 3.3) that are described below.

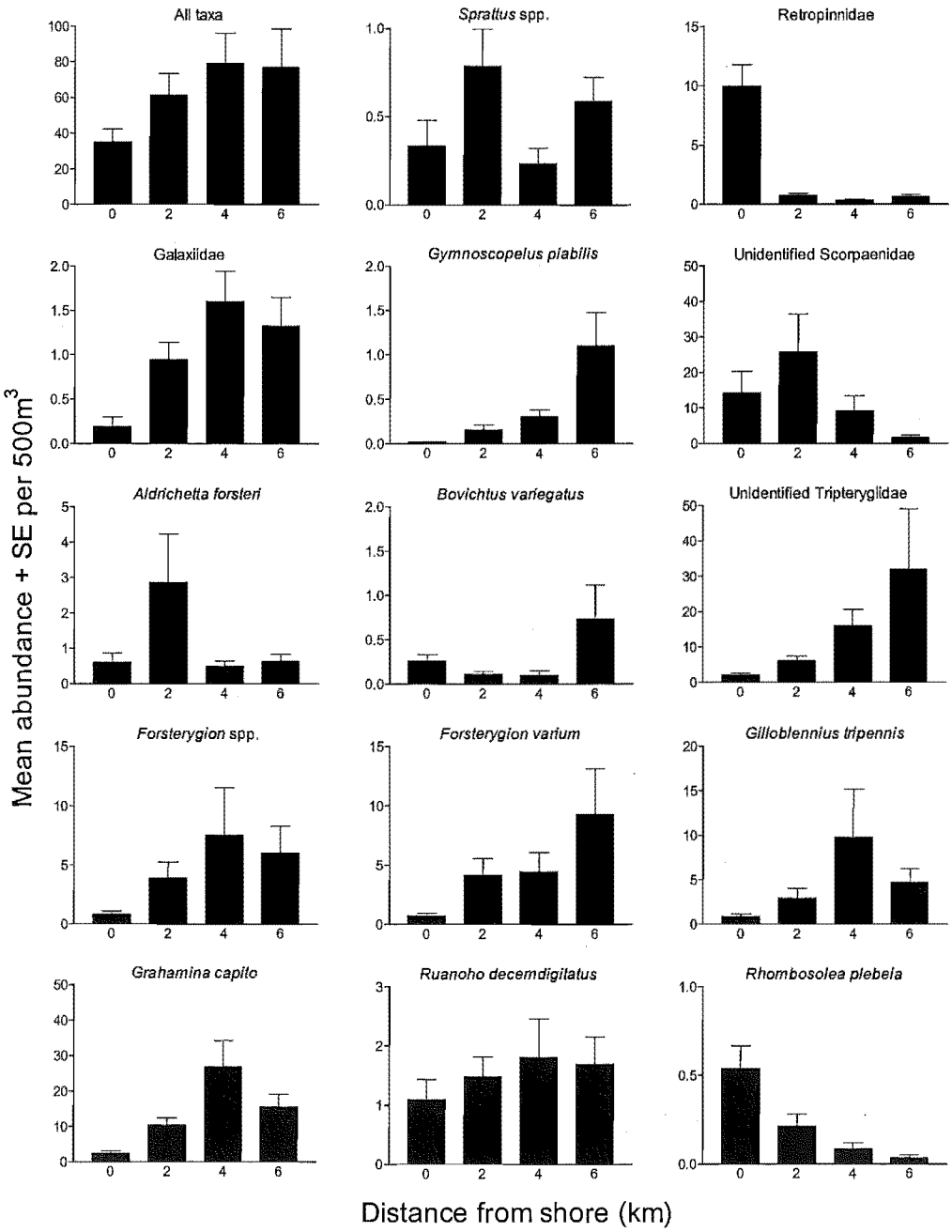

Figure 3.3. Overall mean abundance (+SE) per 500 m^3 of fourteen taxa collected at four stations offshore from the Kaikoura Peninsula between October 1995 and May 1997. n = 111 (37 occasions x 3 replicates) at each station.

When the data were pooled across all occasions, there was little difference among stations in the mean size of larvae from all taxa combined (Fig. 3.4). The mean size of the fourteen common taxa at each of the four stations showed a range of patterns (Fig. 3.4) that are described below.

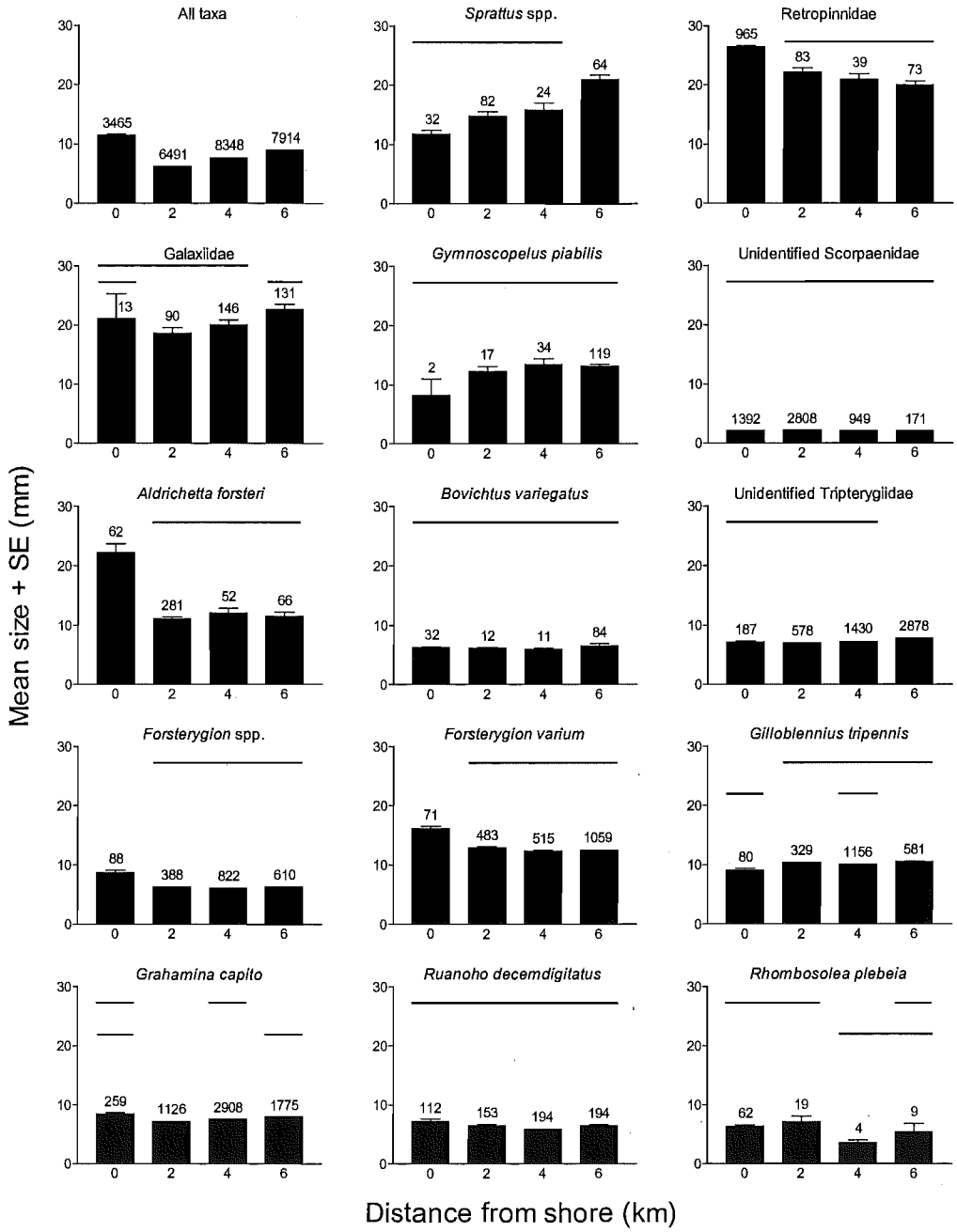

Figure 3.4. The mean size (+SE) (mm) of larvae from fourteen taxa collected between October 1995 and May 1997. The number of larvae that were measured at each station is given. Stations that are under a horizontal line on the same plane are not significantly different (Tukey HSD, $p > 0.05$).

Sprattus spp. larvae were found throughout the year (Fig. 3.5), with a peak in abundance in December/January and a smaller more variable peak in July. Small *Sprattus* spp. larvae (ca. 6.5 mm) appeared in early July and the median size increased until late November (Fig. 3.5). Small larvae appeared again in January suggesting a second spawning event. There was no clear pattern in the number of *Sprattus* spp. larvae with distance offshore (Fig. 3.3). Larvae at the 6 km station had a greater average size than those at the other three stations (Fig. 3.4).

Retropinnid larvae were found from mid-summer until mid-winter (Fig. 3.5), with a peak in abundance in April/May and a smaller peak in July. Small larvae (ca. 10 mm) appeared in January and the median size of larvae increased until May (Fig. 3.5). Small larvae appeared again in June, suggesting a second spawning event. Retropinnid larvae occurred mostly near shore with, on average, ten times more larvae being collected at the 0 km station than at the stations further offshore (Fig. 3.3). Overall, retropinnid larvae at the 0 km station were larger than those collected offshore (Fig. 3.4).

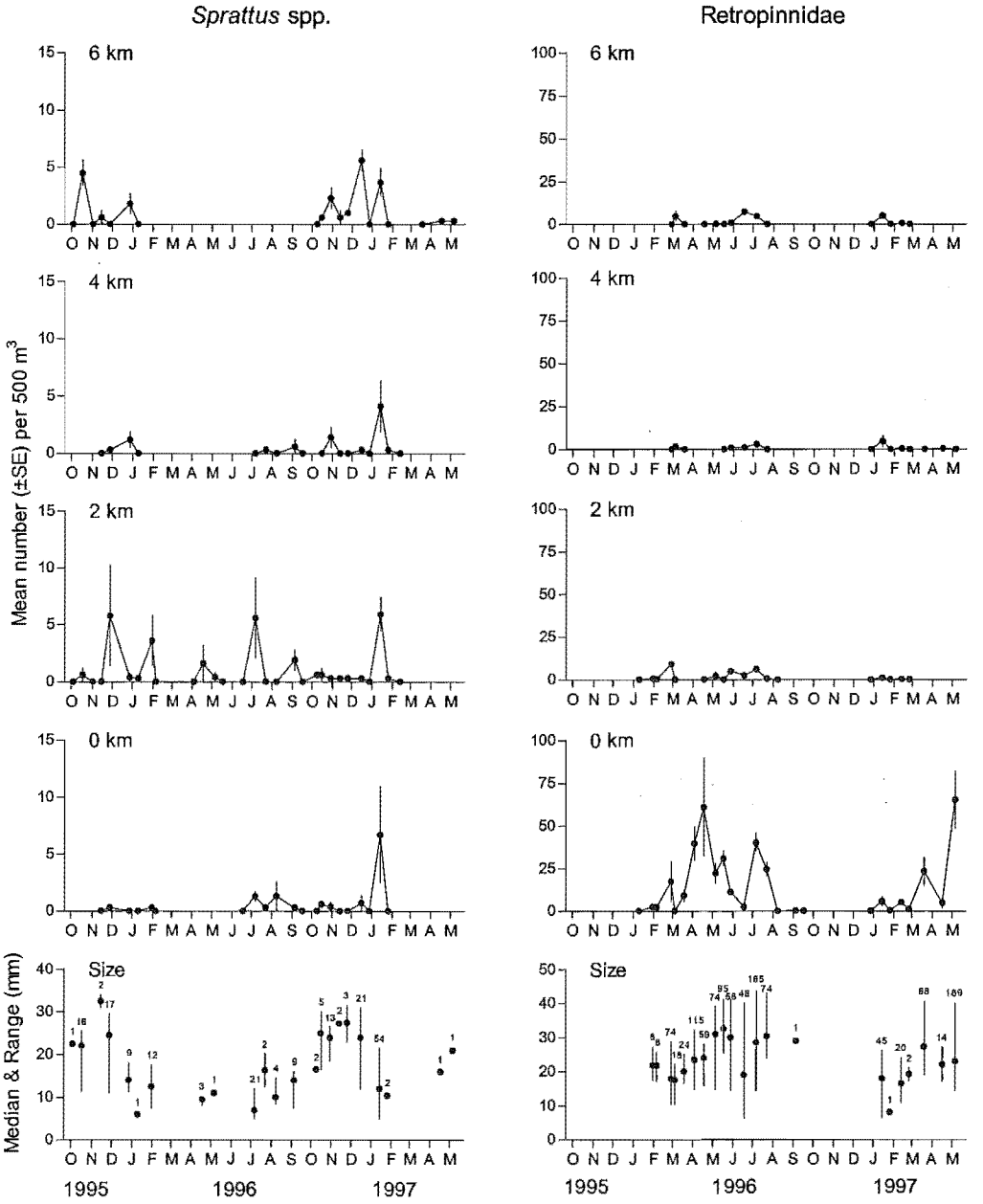

Figure 3.5. Mean number per 500 m^3 (top 4 graphs) and median size (n is shown above each point) and size range (lower graph) of *Sprattus* spp. and retropinnids found at the four stations between October 1995 and May 1997.

Galaxiid larvae were found throughout the year (Fig. 3.6), with a broad peak in abundance in March-May and a smaller peak in July. Small larvae (ca. 6 mm) appeared in January and the median size of larvae increased until May (Fig. 3.6). Small larvae appeared again in late May, suggesting a second spawning event. Galaxiid larvae were most abundant further from shore, with relatively few larvae being collected at the 0 km station compared to the other three stations (Fig. 3.3). Overall, there was little difference in the mean size of galaxiid larvae among stations (Fig. 3.4). Larvae from the 0 km station were highly variable in size, with both the largest and smallest galaxiid larvae being collected there.

Gymnoscopelus piabilis larvae were found from mid autumn until the end of the following spring, with a peak in abundance in October (Fig. 3.6). Small larvae (ca. 5.5 mm) appeared in April, but there was little change in the median size between April and July (Fig. 3.6). Small larvae appeared again in mid October, suggesting a second spawning event. *G. piabilis* larvae were more abundant offshore and few were found at the 0 km station (Fig. 3.3). *G. piabilis* larvae did not vary in size across stations (Fig. 3.4).

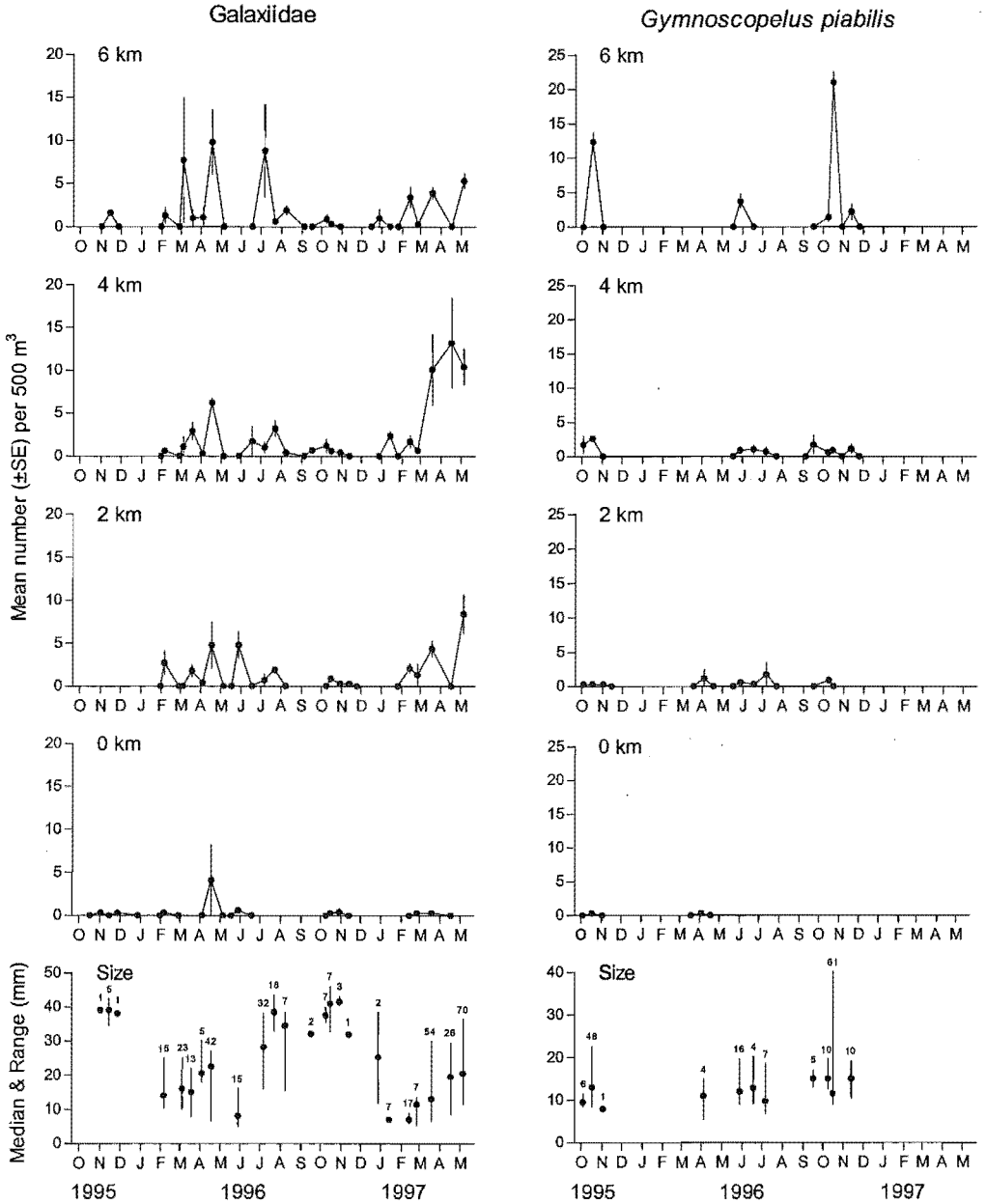

Figure 3.6. Mean number per 500 m^3 (top 4 graphs) and median size (n is shown above each point) and size range (lower graph) of galaxiids and *Gymnoscopelus piabilis* found at the four stations between October 1995 and May 1997.

Unidentified Scorpaenid larvae were found from mid spring until the end of the following autumn, with a peak in abundance in February (Fig. 3.7). Small larvae (ca. 1.5 mm) appeared in October, but there was little change in the median size between October and May (Fig. 3.7). Small larvae (ca. 1.5 mm) were still present in the samples in late February. Large scorpaenid larvae (> 8 mm) were collected only during January and February. Scorpaenid larvae occurred mostly near shore, with few found at the 6 km station (Fig. 3.3). Scorpaenid larvae did not vary significantly in size across stations (Fig. 3.4).

Aldrichetta forsteri larvae were found from mid summer until midway through the following winter, with a peak in abundance in February (Fig. 3.7). Small larvae (ca. 3 mm) appeared in late January and the median size increased until late July (Fig. 3.7). Large numbers of *A. forsteri* larvae were collected at the 2 km station (Fig. 3.3). Overall, *A. forsteri* larvae at the 0 km station were larger than those collected offshore (Fig. 3.4).

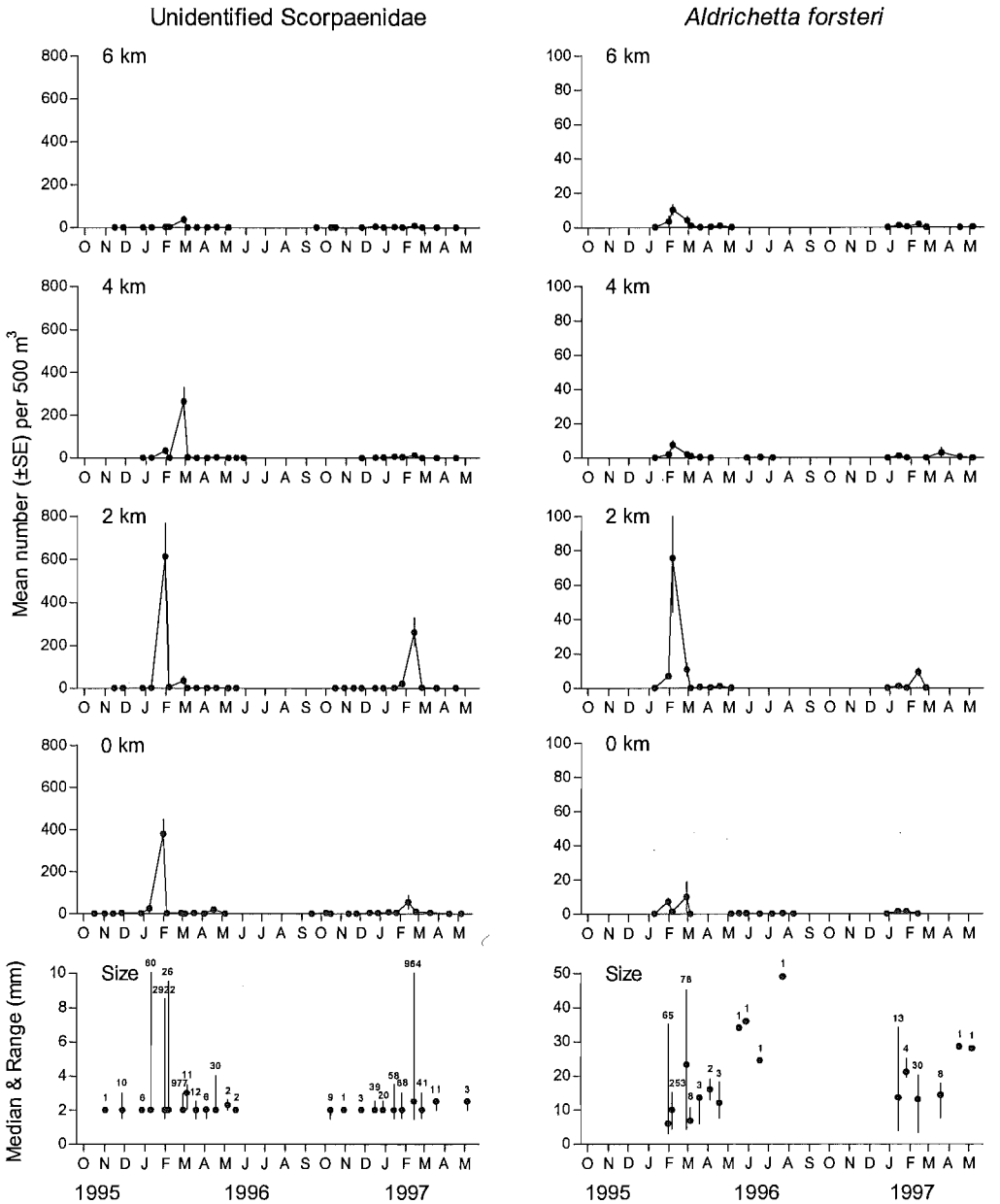

Figure 3.7. Mean number per 500 m^3 (top 4 graphs) and median size (n is shown above each point) and size range (lower graph) of unidentified scorpaenids and *Aldrichetta forsteri* found at the four stations between October 1995 and May 1997.

Bovichtus variegatus larvae were found from late autumn until mid-spring, with a peak in abundance in July at the 6 km station (Fig. 3.8). Small larvae (ca. 4.5 mm) appeared in late May and the median size of larvae increased until late October (Fig. 3.8). Overall, greater but more variable numbers occurred at the 6 km station (Fig. 3.3) and there was no difference in sizes among stations (Fig. 3.4).

Unidentified tripterygiid larvae were found throughout the year, with a peak in abundance in May (Fig. 3.8). Small tripterygiid larvae (ca. 4 mm) appeared in both June and October, with subsequent increases in the median size of larvae (Fig. 3.8). Unidentified tripterygiid larvae became progressively more abundant with distance offshore (Fig. 3.3). Overall, there was no difference in larval sizes among stations (Fig. 3.4).

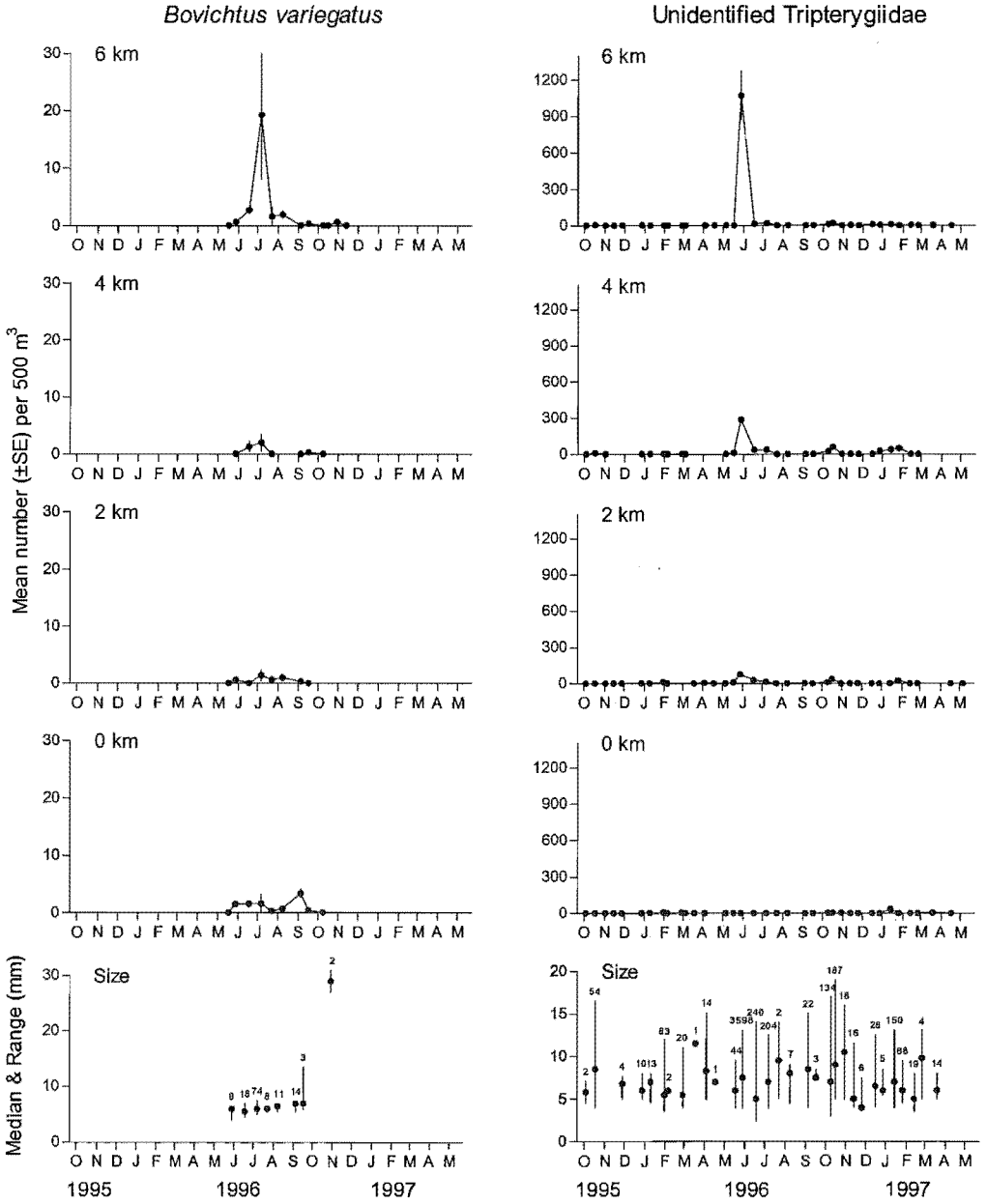

Figure 3.8. Mean number per 500 m^3 (top 4 graphs) and median size (n is shown above each point) and size range (lower graph) of *Bovichtus variegatus* and unidentified tripterygiids found at the four stations between October 1995 and May 1997.

Forsterygion spp. larvae were found from mid spring until mid-autumn, with a peak in abundance in January (Fig. 3.9). Small larvae (ca. 4 mm) appeared in October, but no larvae were found during most of November and December. Small larvae appeared again in late December, suggesting a second spawning event (Fig. 3.9). *Forsterygion* spp. larvae were progressively more abundant offshore to the 4 km station, but numbers at the two furthest stations were highly variable (Fig. 3.3). The few larvae found at 0 km had a slightly larger average size than those at the offshore stations (Fig. 3.4).

Forsterygion varium larvae were found throughout the year, with a peak abundance in May (Fig. 3.9). Small larvae (ca. 4.5 mm) appeared in late May, October and November with subsequent increases in the median size (Fig. 3.9). *F. varium* larvae were progressively more abundant offshore (Fig. 3.3). The larvae at 0 km had a greater average size than those at the other three stations (Fig. 3.4).

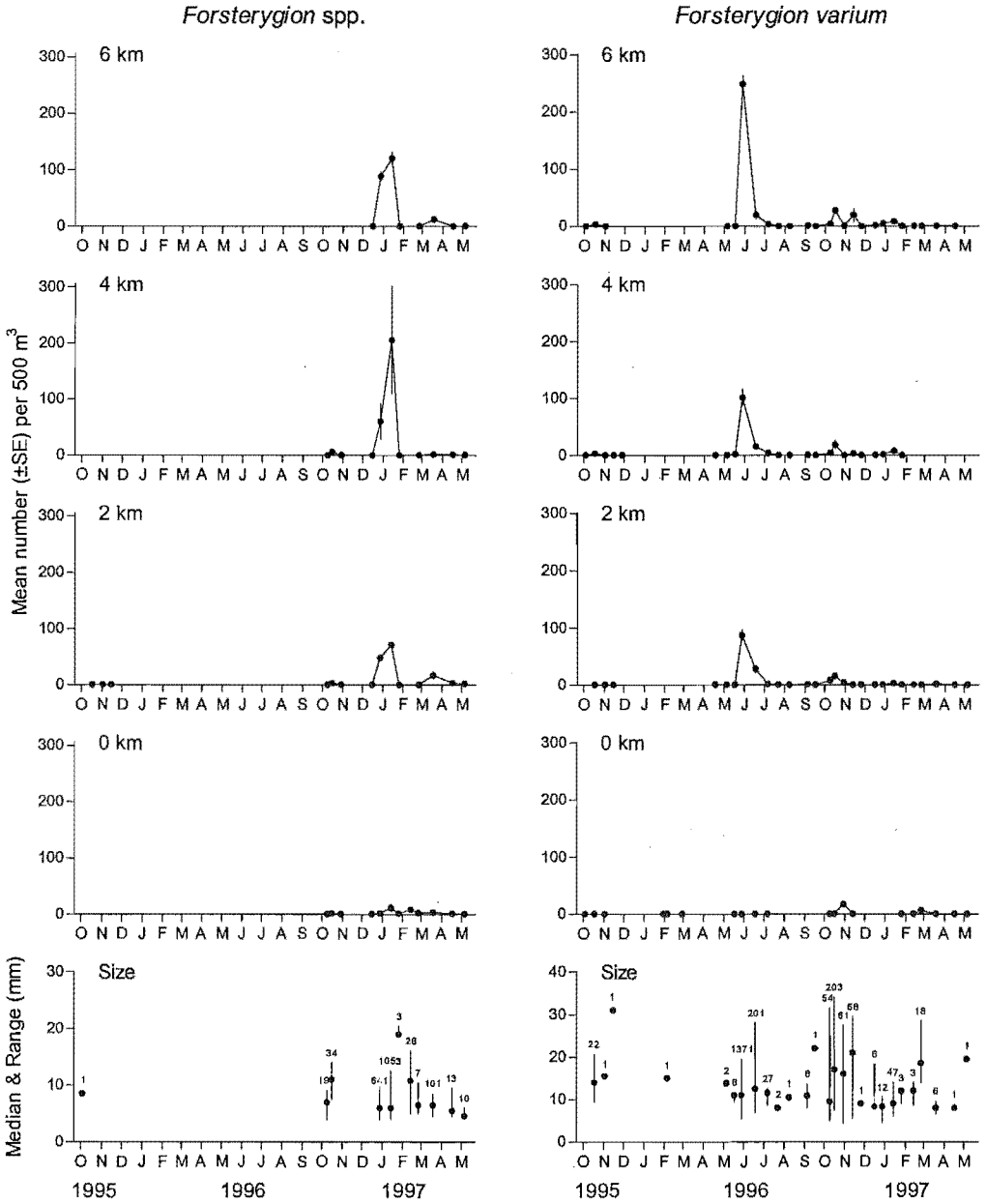

Figure 3.9. Mean number per 500 m^3 (top 4 graphs) and median size (n is shown above each point) and size range (lower graph) of *Forsterygion* spp. and *Forsterygion varium* found at the four stations between October 1995 and May 1997.

Gilloblennius tripennis larvae were found throughout the year except in mid-winter, with a peak in abundance in October (Fig. 3.10). Small larvae (ca. 4 mm) appeared in September and the median size of larvae increased until December. Small larvae appeared again in January/February, suggesting a second spawning event (Fig. 3.10). *G. tripennis* larvae were most abundant at the 4 km station and least abundant inshore. Larvae were about the same size at all stations (Fig. 3.4).

Grahamina capito larvae were found from early spring through until late summer, with a peak in abundance in January (Fig. 3.10). Small larvae (ca. 3.5 mm) appeared in September, but there was no increase in the median size of larvae until after a second influx of small larvae in January/February (Fig. 3.10). *G. capito* larvae were most abundant at the 4 km station and least abundant inshore (Fig. 3.3). Larvae were about the same size at all stations (Fig. 3.4).

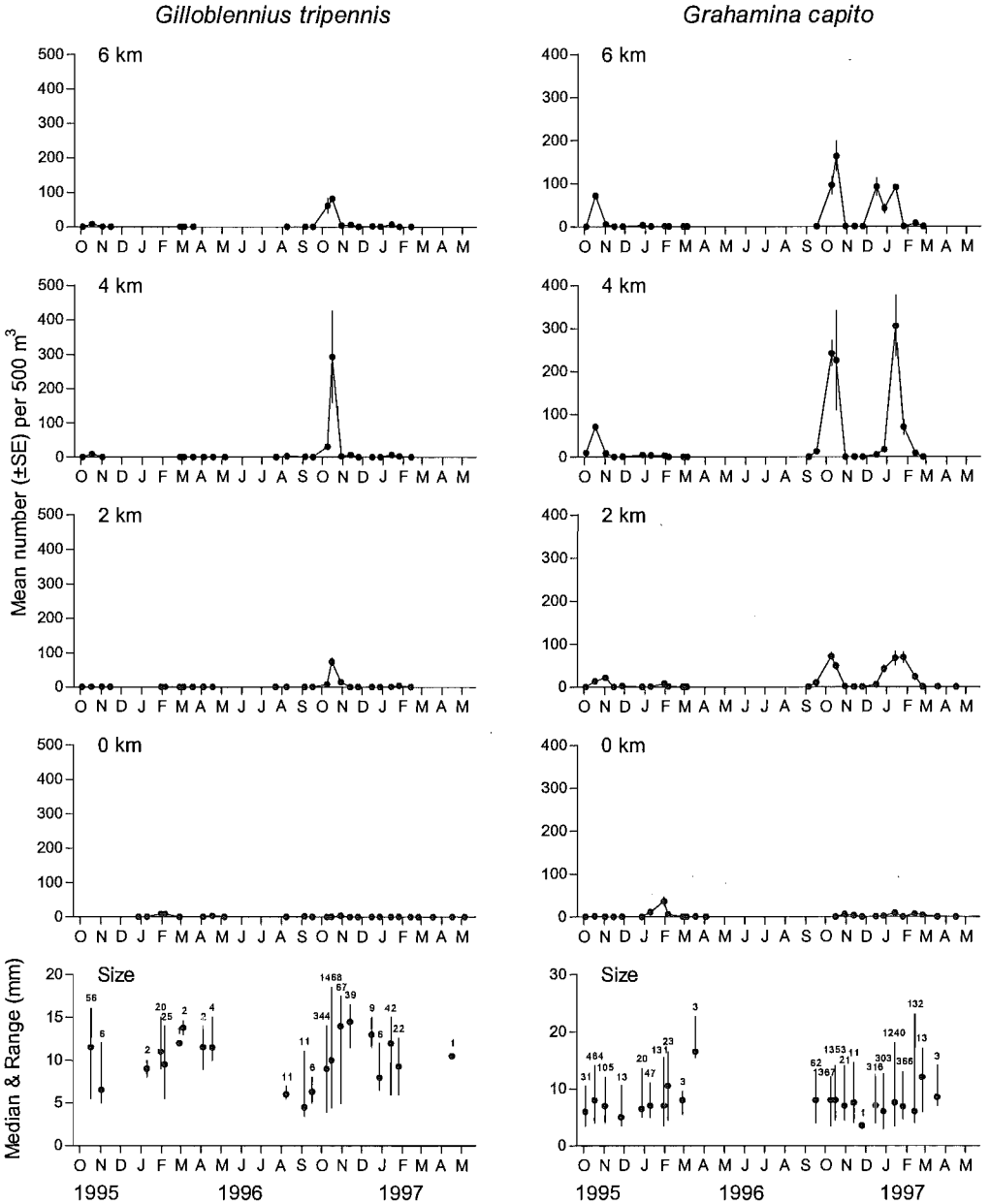

Figure 3.10. Mean number per 500 m^3 (top 4 graphs) and median size (n is shown above each point) and size range (lower graph) of *Gilloblennius tripennis* and *Grahamina capito* found at the four stations between October 1995 and May 1997.

Ruanoho decemdigitatus larvae were found throughout the year except for mid-winter (June-August), with a peak in abundance in January (Fig. 3.11). Small larvae (ca. 3.5 mm) appeared throughout much of spring and summer (Fig. 3.11). Numbers were variable within each station and there were no great differences among stations (Fig. 3.3). Larvae were generally the same size at all stations (Fig. 3.4).

Rhombosolea plebeia larvae were found throughout most of the year, with a peak in abundance in October and in January/February (Fig. 3.11). Small larvae (ca. 2.5 mm) appeared at various times throughout the year and consequently there was no clear pattern in the size of larvae through time (Fig. 3.11). *R. plebeia* larvae became progressively less abundant with distance offshore (Fig. 3.3). Overall, there was little difference in the mean sizes of *R. plebeia* larvae among stations (Fig. 3.4).

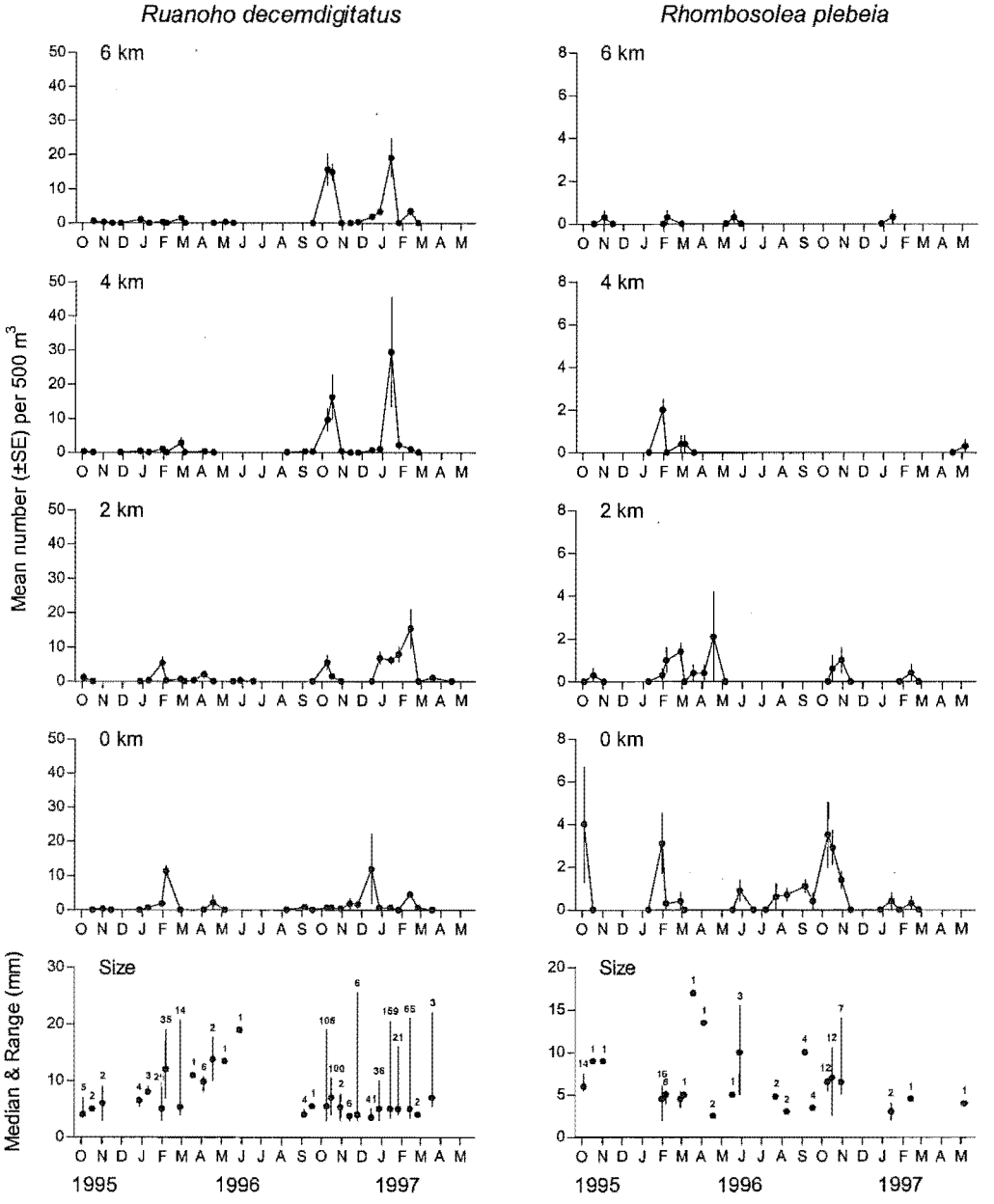

Figure 3.11. Mean number per 500 m^3 (top 4 graphs) and median size (n is shown above each point) and size range (lower graph) of *Ruanoho decemdigitatus* and *Rhombosolea plebeia* found at the four stations between October 1995 and May 1997.

The size-frequency distribution of the total tripterygiid larvae at each station was skewed to the right (Fig. 3.12). Most of the tripterygiid larvae at the three offshore stations were between 5 and 12 mm, but larger larvae (up to 32 mm) were also present. Very small larvae (3-4 mm) and larvae in the 10-20 mm size range were found more frequently at the 0 km station than at the offshore stations.

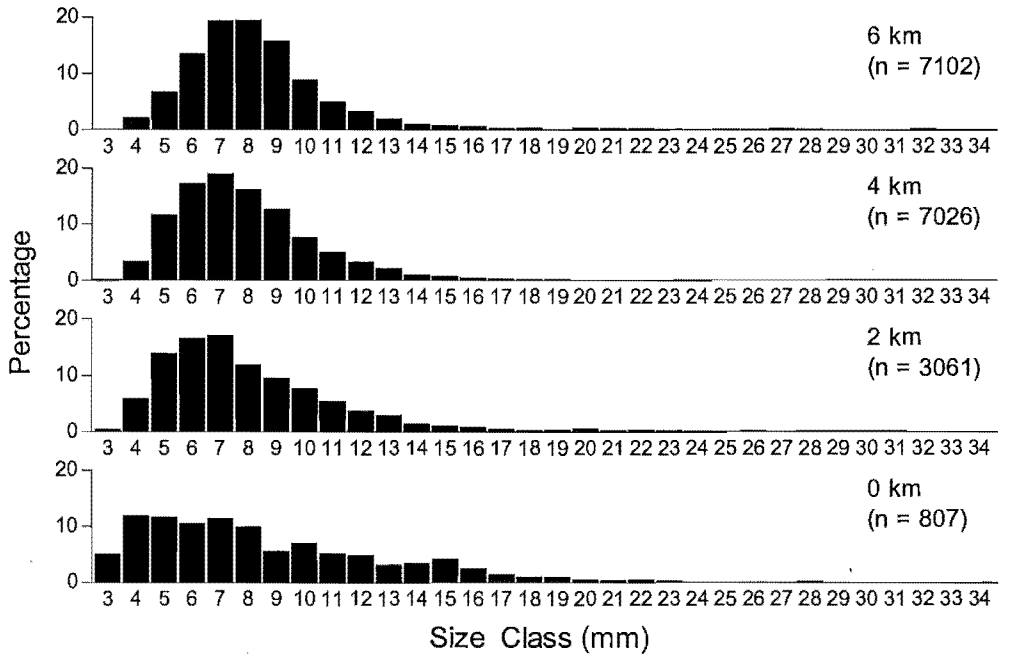

Figure 3.12. Size-frequency (%) distributions of all tripterygiid larvae collected at the four stations between October 1995 and May 1997. Sizes have been rounded down to the nearest mm (n = the number of larvae that were measured at each station).

When the data from all four stations were combined and fortnightly samples were averaged to produce monthly mean abundances, groupings of taxa with similar temporal distributions emerged (Fig. 3.13). Absolute abundances varied considerably between taxa, but most had an obvious peak in abundance during one month of the year, while some had a second peak at another time.

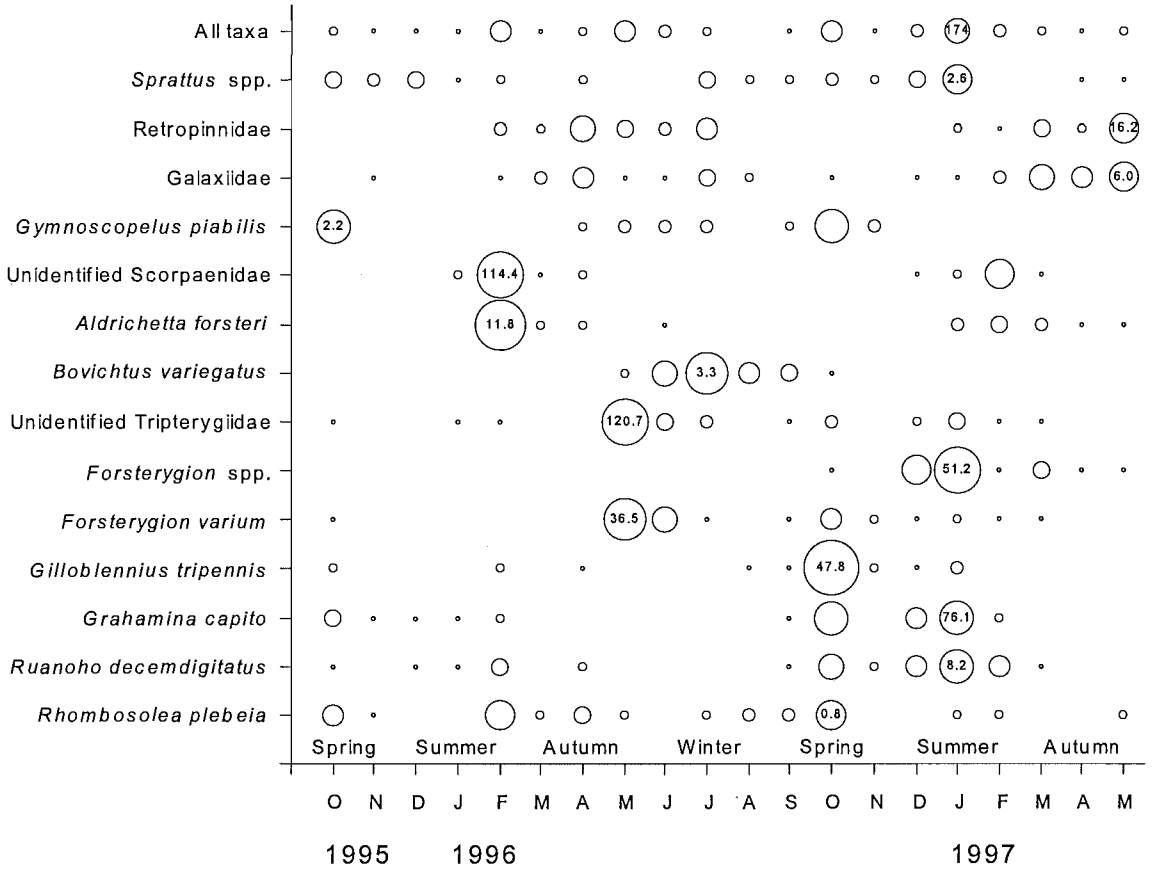

Figure 3.13. Temporal distribution of fourteen common taxa sampled between October 1995 and May 1997. For each taxon, the bubble area represents the percentage of the total catch of that taxon that was caught in each month. Because abundances are expressed as percentages for a taxa through time, taxa bubbles cannot be directly compared across taxa within months. Peak abundances (per 500 m^3) are given inside the appropriate bubble for each taxon.

The monthly mean abundances of several of the common taxa were positively correlated (Table 3.5). In examining the overall similarity of samples, there were discrete clusters identified from a PCA (Fig. 3.14). The PCA bi-plot can be interpreted by drawing a line through each taxon point and the origin (0,0). This line is then the imaginary axis for that taxon. When monthly samples are projected onto this axis, those whose projection point is closest to the taxon point contained the highest abundance of that particular taxon. Similarly, the projection points of other taxa onto the imaginary axis will yield a ranking of correlations with the taxon that forms the imaginary axis. In this ranking, the origin indicates zero correlation.

Table 3.5. Pearson correlation coefficients for 14 common taxa using 20 monthly mean abundances. Data were log (x+1) transformed prior to correlation. Significant correlations are shown in bold. α level has been corrected for multiple comparisons: ($\alpha = \frac{0.05}{91} = 0.00549$, $r_{0.00549(2),18} = 0.703$).

	Retropinnidae	Galaxiidae	*Gymnoscopelus piabilis*	Unidentified Scorpaenidae	*Aldrichetta forsteri*	*Bovichtus variegatus*	Unidentified Tripterygiidae	*Forsterygion* spp.	*Forsterygion varium*	*Gilloblennius tripennis*	*Grahamina capito*	*Ruanoho decemdigitatus*	*Rhombosolea plebeia*
Sprattus spp.	-0.224	-0.396	0.121	0.004	-0.041	0.074	0.252	0.513	-0.026	0.362	0.650	0.544	0.114
Retropinnidae		**0.768**	-0.209	0.055	0.206	0.246	0.201	0.023	0.118	-0.347	-0.490	-0.199	-0.047
Galaxiidae			-0.279	-0.046	0.074	0.021	-0.281	0.083	-0.250	-0.298	-0.508	-0.249	-0.131
Gymnoscopelus piabilis				-0.336	-0.252	0.048	0.357	-0.225	0.454	0.692	0.402	0.135	0.619
Unidentified Scorpaenidae					**0.848**	-0.337	-0.044	0.196	-0.245	-0.002	0.300	0.544	0.288
Aldrichetta forsteri						-0.203	-0.012	0.072	-0.187	0.034	0.118	0.364	0.458
Bovichtus variegatus							0.315	-0.262	0.246	-0.175	-0.347	-0.330	-0.119
Unidentified Tripterygiidae								0.223	**0.888**	0.265	0.265	0.331	0.150
Forsterygion spp.									0.042	0.134	0.529	0.652	-0.213
Forsterygion varium										0.271	0.100	0.162	0.053
Gilloblennius tripennis											0.690	0.626	**0.714**
Grahamina capito												**0.840**	0.430
Ruanoho decemdigitatus													0.369

Each of the four clusters (Fig. 3.14) represents a different temporal distribution pattern. Unidentified scorpaenids and *A. forsteri* (Scorp and Aldri) occurred during slightly different periods (Fig. 3.13), but each had a single peak in abundance in late summer (February). Galaxiids and retropinnids (Galax and Retro) co-occurred during similar periods (Fig. 3.13), with each having a peak in abundance in mid to late autumn (April/May) followed by a second slightly smaller peak in mid-winter (July). *B. variegatus* (Bovic) was the only taxon to have a single peak in abundance in mid-winter (July). Unidentified tripterygiids, *F. varium* and *G. piabilis* (Tript, Fvari and Gymno) each occurred throughout most of the year (Fig. 3.13), with peaks in abundance in late autumn (May) and in mid-spring (October). The remaining common taxa each had abundance peaks in mid-spring (October) and/or mid-summer (January).

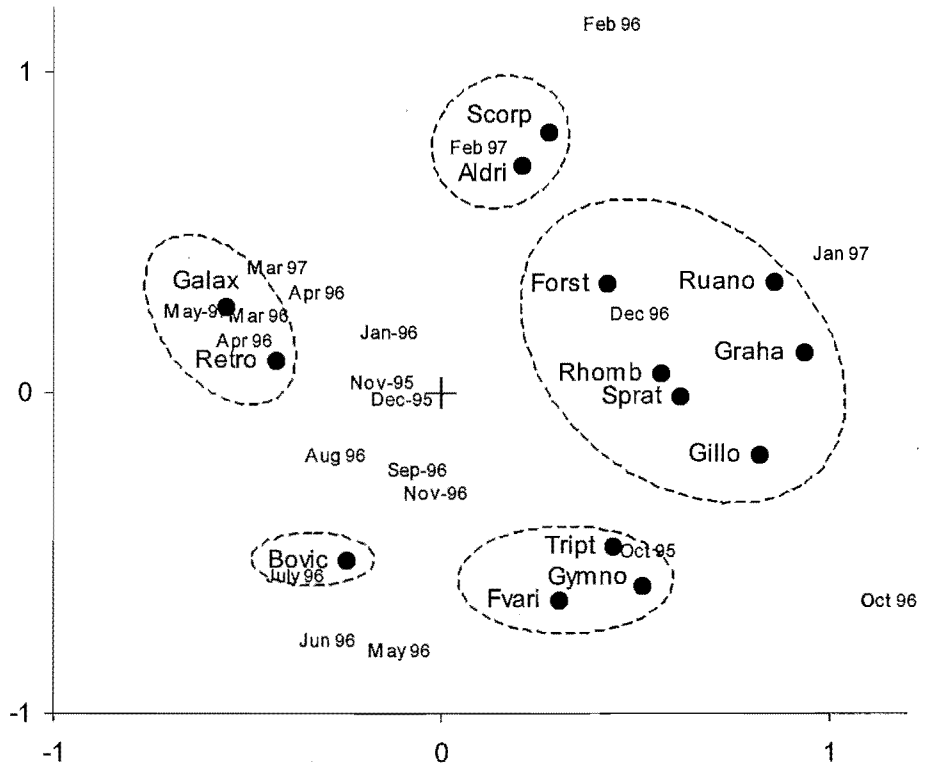

Figure 3.14. Correlation bi-plot based on Principal Components Analysis of the monthly mean abundance data. Dates indicate monthly mean samples and taxon codes are the first five letters of the genus or family of the 14 common taxa (except Fvari for *F. varium*). Dotted circles indicate groupings of positively correlated taxa.

3.3.2 Physical parameters

Overall, surface water temperature did not differ significantly between the four stations ($F_{3,296} = 0.61$, $p = 0.607$), so the data from all stations were grouped on each sampling occasion. Surface water temperature varied significantly during the year ($F_{36,407} = 399.95$, $p < 0.001$), reaching a maximum temperature of 17.6 °C on 1st February 1996 and a minimum of 9.4 °C on 9th August 1996 (Fig. 3.15). Average daily wind speeds fluctuated markedly during the year (Fig. 3.16), but there was no significant difference between months in average wind speed ($F_{20,618} = 1.26$, $p = 0.202$). Average daily wind direction differed between seasons ($\chi^2 = 184.768$, $df = 21$, $p < 0.001$) changing from predorninately E/NE winds in summer to W/SW winds in the winter (Fig. 3.17).

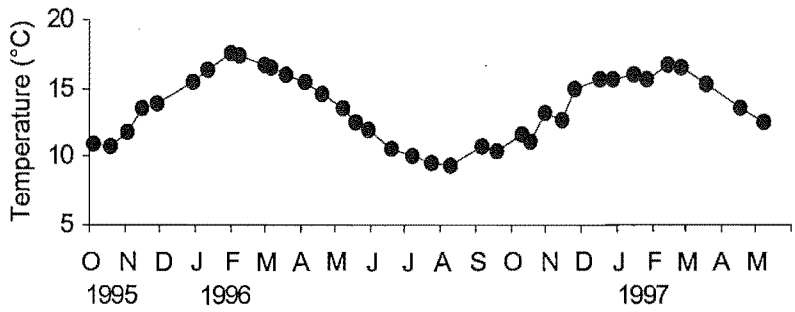

Figure 3.15. Mean sea surface temperature in the study area between October 1995 and May 1997. Each point represents the mean of the four sampling stations.

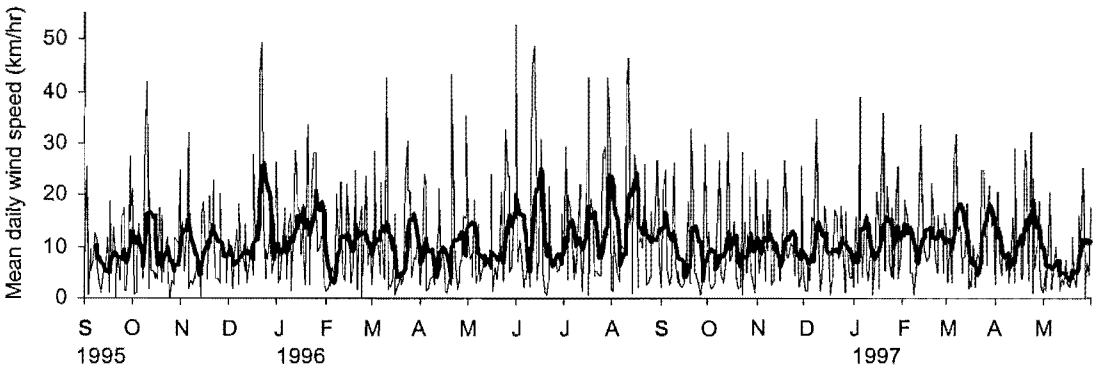

Figure 3.16. Mean daily wind speed (km/hr) and seven day moving average between September 1995 and May 1997. Data are from the Kaikoura automated weather station (G23464).

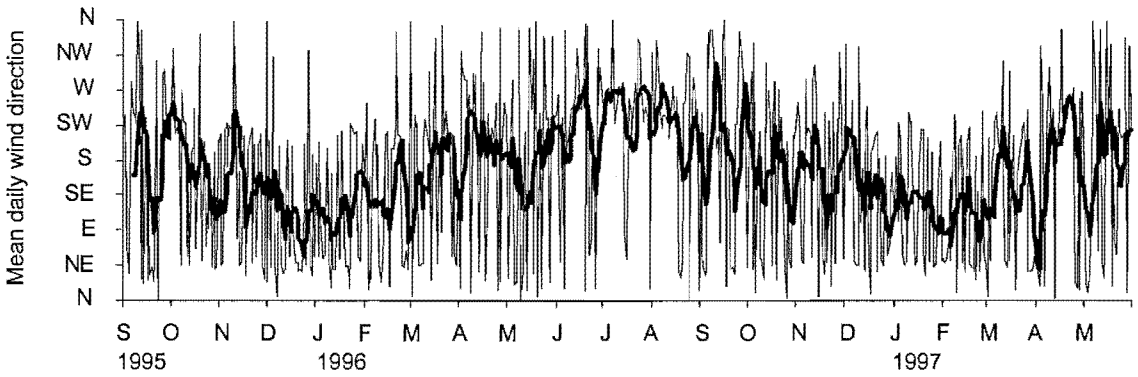

Figure 3.17. Mean daily wind direction and seven day moving average between September 1995 and May 1997. Data are from the Kaikoura automated weather station (G23464).

Average wind speed correlated poorly with the number of individual taxa that were collected. When the average wind speed over the 24 hr period immediately prior to sampling (i.e., prior to 0700 hrs on the day of sampling) was correlated with the total number of each of the most common taxa caught at the 4 stations, only galaxiids showed a significant degree of association ($r = -0.415$, $p < 0.05$). This result suggests that fewer galaxiids were caught following periods of strong wind. However, a closer examination of the data suggests that seasonal fluctuations in the abundance of galaxiids may be confounding this pattern, with fewer larvae being caught in non-autumnal seasons, regardless of wind speed (Fig. 3.18).

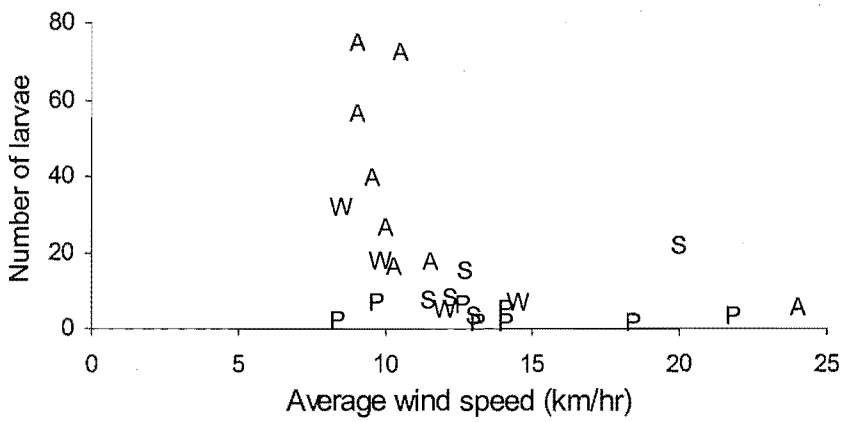

Figure 3.18. Number of galaxiids caught at all stations versus the average wind speed in the 24 hours prior to sampling. Data points are coded according to season: autumn (A), winter (W), spring (P) and summer (S).

3.3.3 Phytoplankton and zooplankton production

Measurements of primary- and zooplankton production were not made during the course of this study. However, extensive productivity data have previously been recorded in the area by Grieve (1966). She sampled a permanent station in 200 m of water, approximately 8 km due east of the Kaikoura Peninsula, over a twelve-month period. Her data showed a peak in phytoplankton production (chlorophyll *a*) during early spring (September/October) and a smaller, less defined peak in late summer (February/March) (Fig. 3.19).

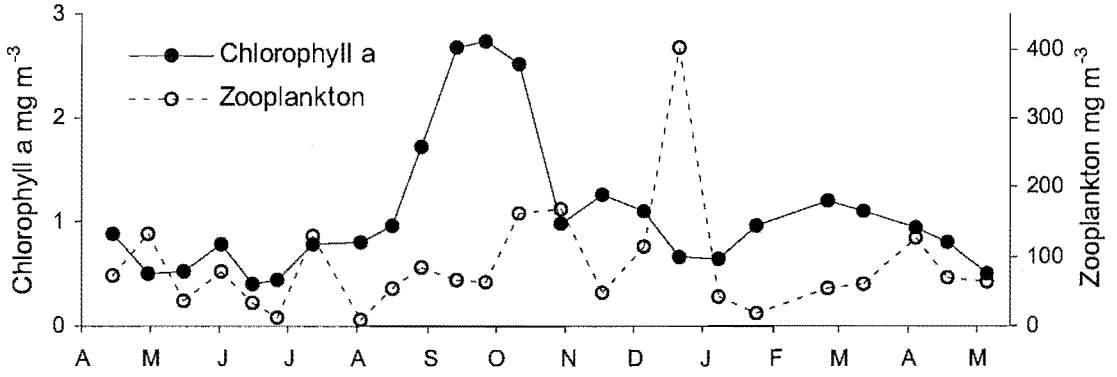

Figure 3.19. Seasonal cycle of Chlorophyll *a* (mg m^{-3}) and zooplankton biomass (wet weight mg m^{-3}) at the Kaikoura permanent station between April 1964 and May 1965 (from Grieve (1966)). Chlorophyll *a* data are the mean of tows at four depths (0, 10 ,25 and 50 m). Zooplankton biomass are from oblique hauls from 200 m.

Total zooplankton biomass fluctuated greatly during the year, but increased markedly during spring and peaked in early summer (Fig. 3.19). The numbers of Copepoda also fluctuated greatly during the year (Fig. 3.20). The greatest numbers occurred in September, October and February and were concentrated in the surface waters.

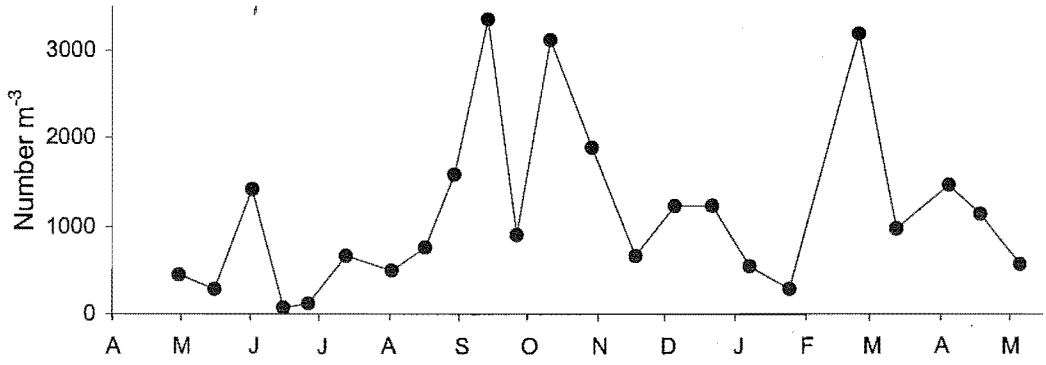

Figure 3.20. Seasonal cycle of Copepoda abundance (numbers m^{-3}) at the Kaikoura permanent station between April 1964 and May 1965 (from Grieve (1966)). Data are the mean of horizontal tows at four depths (5, 22, 70 and 120 m).

3.4 DISCUSSION

The ichthyoplankton collected during this study reflect the diverse fish fauna in the Kaikoura region. Oceanic currents and the nearby Kaikoura canyon contribute oceanic and deep-dwelling species to the already large array of coastal and reef fish species. However, most of the 58 taxa collected during this study were relatively rare. This apparent rarity may be real or it may be a consequence of the sampling procedure. The abundance of taxa that do not

commonly inhabit the neuston layer will be underestimated by the sampling protocol used in this study. Furthermore, the abundance of a taxon that occurred in a temporal pulse on a scale finer than that which was sampled (< 2 weeks) would also be underestimated. However, 14 taxa were sufficiently common in the samples to allow analysis of the temporal and spatial patterns in their abundance.

3.4.1 Temporal distribution

A single major peak of abundance during the year is typical of the larvae of fish in temperate and sub-arctic waters (Jenkins 1986, Ferreiro & Labarta 1988, Haldorson *et al.* 1993). This peak has been linked strongly to annual production cycles in Cushing's (1975) match/mismatch hypothesis. This hypothesis assumes that the production of fish larvae in temperate waters generally coincides with phytoplankton blooms and peak reproduction of zooplankton in spring and autumn. Many studies have observed fish larval abundance peaks that coincide with maximum zooplankton densities (Townsend 1984, Jenkins 1986, Haldorson *et al.* 1993, Horstman & Fives 1994). The strategy of synchronising production of larvae with periods of high prey abundance has obvious adaptive value. Fish species that engage in this strategy were described as being "synchronous" by Sherman *et al.* (1984). Alternatively, those with a more prolonged period of larval production have been described as "bet-hedging" (Lambert & Ware 1984) or "ubiquitous" (Sherman *et al.* 1984). This strategy is likely to be adaptive in localities where prey supply is erratic (Sherman *et al.* 1984).

Given the phytoplankton and zooplankton production cycles described by Grieve (1966) for the Kaikoura region, the fish taxa that were common in the neuston appear to follow two different reproductive strategies. One group, which has peaks in abundance in spring or summer or both (*Sprattus* spp., unidentified scorpaenids, *A. forsteri*, *Forsterygion* spp., *G. tripennis*, *G. capito*, *R. decemdigitatus* and *R. plebeia*) is clearly synchronous as defined above. A second group, which has peaks in abundance in mid to late autumn (galaxiids and retropinnids) and in mid-winter (*B. variegatus*), could be termed "early". This strategy was defined by Haldorson *et al.* (1993) as being used by those species that produce their larvae prior to the peak in the spring phytoplankton bloom. The three taxa (unidentified tripterygiids, *F. varium* and *G. piabilis*) that had a prolonged production of larvae could be classed as bet-hedgers.

Because this study extended over two years, it allowed an assessment of the inter-annual variation in the timing and amplitude of larval abundance. Most of the common taxa were relatively consistent between years in the timing of their abundance peaks. However, few were consistent in the amplitude of these peaks. *G. capito* had abundance peaks in mid-spring and mid-summer in both years of this study. However, abundances in October 1995 and January 1996 differed markedly from matching peaks in October 1996 and January 1997. Unidentified scorpaenids, *A. forsteri*, *Forsterygion* spp. and *R. decemdigitatus* also showed large inter-annual variability in larval abundance. This variability in larval supply will have a major influence on the structure and dynamics of local populations.

The temporal distribution of ichthyoplankton has not previously been studied in southern New Zealand. However, several studies have examined the appearance and disappearance

during the year of individual taxa in the ichthyoneuston off northeastern New Zealand (see review by Kingsford 1988). It was thought that the geographic separation of the present study from those done off northeastern New Zealand, together with very different current and exposure regimes, was likely to result in marked differences in the temporal distribution of ichthyoplankton of shared taxa. However, the majority of shared taxa (especially the tripterygiids) showed similar temporal abundance patterns between locations. In some cases (e.g., *R. decemdigitatus*), the two locations shared the spring peak in abundance of a taxon, but the late summer peak was missing or less distinct in the northern studies (Thompson 1983, Roper 1986).

One notable exception to the synchrony between locations was the temporal distribution of *A. forsteri*. In a study off northeastern New Zealand, Tricklebank *et al.* (1992) estimated maximum densities of 45 *A. forsteri* per 300 m^3 in November 1986. In a similar area, Kingsford & Choat (1986) recorded maximum densities of 429 per 100 m^3 in the slicks of internal waves in November-December 1984. However, I collected no *A. forsteri* during October, November or December. Instead, I recorded a large abundance peak in early February and a much smaller peak in April. *A. forsteri* of all sizes (4-31 mm) have been found in the neuston (Kingsford & Tricklebank 1991), so it would seem unlikely that this species was present but not sampled in my study. Therefore, it appears that either the initial spawning of *A. forsteri* in the Kaikoura region is markedly delayed or that *A. forsteri* eggs take considerably longer to hatch compared to northern stocks.

3.4.2 Spatial distribution

Many studies have shown that the abundance of ichthyoplankton varies with distance from shore (Koubbi *et al.* 1991, Suthers & Frank 1991, Boehlert & Mundy 1994, MacGregor & Houde 1996, Grioche & Koubbi 1997). In my study, the greatest abundances of fish larvae were found further offshore (4 km and 6 km). The most common taxa offshore included deep water species (*G. piabilis)*, freshwater species (galaxiids) and several intertidal/reef species (*B. variegatus* and most of the tripterygiids). Other taxa showed no clear pattern with distance offshore (*Sprattus* spp. and *R. decemdigitatus*) or were more abundant closer to shore (retropinnids, unidentified scorpaenids, *A. forsteri* and *R. plebeia*).

Several authors have found that larvae that are more abundant nearshore hatch from demersal eggs, whereas those that are more widely distributed are generally derived from pelagic eggs (Leis & Miller 1976, Marliave 1986, Kingsford & Choat 1989, Suthers & Frank 1991, Brogan 1994a, Gray 1998). The nearshore abundance of larvae hatched from demersal eggs is thought to be due to the absence of passive drift during the egg phase. While data presented in this study support these patterns for some taxa (e.g. both *Sprattus* spp. and *A. forsteri* hatch from pelagic eggs and their larvae were widely dispersed) others do not follow the patterns observed elsewhere. Most of the taxa (the galaxiids and tripterygiids) that hatch from demersal eggs were more abundant at the offshore stations and *R. plebeia*, which hatch from pelagic eggs, were more abundant nearshore.

Several authors have reported greater numbers of tripterygiids at nearshore sites (Leis & Miller 1976, Leis 1982, Gray 1993), particularly in the vicinity of reefs (Leis & Goldman 1984, Kingsford & Choat 1989, Brogan 1994a). However, in my study most taxa within the family Tripterygiidae showed equal if not greater abundance at the offshore stations than at the nearshore station. Furthermore, tripterygiid larvae of all sizes (3 - 32 mm) were found at the offshore stations. Clearly, the data in my study do not support the assertion that tripterygiid larvae are more abundant nearshore. The reasons for this discrepancy may be temporal or methodological.

The influence of the season of sampling on estimates of offshore distribution of tripterygiid larvae was alluded to by Tricklebank *et al.* (1992). They suggested that researchers who sampled only during spring or summer (i.e. Leis 1982, Leis & Goldman 1984, Kingsford & Choat 1989) found highest abundances of tripterygiid larvae nearshore. However, their samples taken during winter on similar spatial scales (and in the case of Kingsford & Choat (1989) in the same location) contained much greater numbers of tripterygiid larvae, and these larvae were found in peak densities offshore rather than nearshore (Tricklebank *et al.* 1992). The data in my study support that pattern, with very large numbers of tripterygiid larvae being found in mid-winter samples, particularly offshore. However, some nearshore summer samples (particularly January/February 1996) contained greater abundances of tripterygiid larvae (especially *G. tripennis*, *G. capito* and *R. decemdigitatus*) than the associated offshore samples. If sampling was done only at this time, a very different pattern of offshore distribution would be perceived.

Many of the studies reporting greater numbers of tripterygiid larvae offshore used oblique tows to sample ichthyoplankton (Leis 1982, Kingsford & Choat 1989, Brogan 1994a). The only other study that reported greater numbers of tripterygiid larvae offshore also used surface tows (Tricklebank *et al.* 1992). Kingsford (1986) found that oblique tows grossly underestimated the abundance of tripterygiid larvae because these larvae are more abundant in surface waters. In shallower water, however, tripterygiid larvae have a broader depth distribution (see Kingsford (1986) and Chapter 5) and therefore may be sampled better by oblique hauls than surface hauls. It is likely that oblique hauls underestimate the abundance of tripterygiid larvae at offshore sites and that surface tows underestimate the abundance of tripterygiid larvae at nearshore sites.

The anadromous retropinnids occurred almost exclusively at the nearshore station. This taxon's ability to maintain this distribution is most likely a result of its life history. Adult retropinnids spawn in rivers, releasing eggs which then sink to the substrate (McDowall 1990). The eggs develop there and, after hatching, the larvae are carried out to sea by river currents. Larvae are about 5 mm in length when they hatch (McMillan 1961), so it is likely that by the time they reach the sea they are capable swimmers. It has been suggested that fish larvae that are larger at hatching and at a more advanced stage of development because of hatching from demersal eggs may be more capable of remaining within a given area by using their superior swimming and sensory abilities (Suthers & Frank 1991). For retropinnids, the lack of planktonic dispersal while in the egg phase coupled with a stronger swimming ability may allow them to restrict their distribution to nearshore areas.

The offshore distribution of the retropinnids contrasts markedly with that of the galaxiids. Galaxiid larvae disperse widely, with few larvae occurring close to shore (0 km). The differing spatial distribution of these two families may reflect differing needs in terms of using the planktonic phase as a dispersal mechanism. The galaxiids, like the retropinnids, are diadromous. However, they are mostly amphidromous. The larvae of amphidromous species migrate to sea soon after hatching to feed and grow to a post-larval stage. Juveniles then migrate back into freshwater where most somatic growth, as well as sexual maturation and reproduction, occurs (McDowall 1997). For anadromous species like the retropinnids, most feeding and growth is at sea prior to the migration of fully grown adult fish into freshwater to reproduce. Retropinnids are short-lived (1-2 years) and can disperse widely as juveniles and adults during their extended period at sea. Galaxiids are much longer-lived (up to 30 yrs) and are likely to need their planktonic phase as a dispersal mechanism so that post-larval stages can restore populations in perturbed river systems (McDowall 1996). The positioning of galaxiid ichthyoplankton further from shore aids in this dispersal.

Larvae of both reef and freshwater fish species must eventually move closer to shore to settle successfully from their planktonic phase to a more sedentary existence on reefs or to migrate into rivers. Clearly, taxa such as the galaxiids and tripterygiids, which occurred in relatively high abundances further from shore, must move nearer to shore as they develop. The mechanisms of the onshore transport of fish larvae in the Kaikoura region are not yet known, but may include internal waves (Kingsford & Choat 1986), wind-derived water motion (Heath 1972b), or eddies (Lobel & Robinson 1986). While the mechanisms of this shoreward transport are currently unknown, there is clear evidence from several taxa in this study of larger (and therefore older) larvae occurring closer to shore. These are likely to be the few remaining survivors from the more abundant, but younger, larval assemblages seen further offshore.

Chapter Four

Alongshore Distribution Patterns of Larval Fish

4.1 INTRODUCTION

Reef fish may disperse widely during their planktonic larval phase. Dispersal of larval reef fish is considered to offer an adaptive advantage, but there is disagreement as to the nature of this advantage. Johannes (1978) suggested that planktonic dispersal enables larvae to avoid planktivorous reef fish. Barlow (1981) asserted that planktonic dispersal gives reef fish species the ability to migrate in their early life stages between the patchy environments that adults inhabit but cannot bridge. Doherty *et al.* (1985) argued that substantial larval dispersal is adaptive when the propagules experience uneven and unpredictable survival in the pelagic environment. In this situation, substantial dispersal is a means of risk-spreading in a heterogeneous space, even though dispersal may incur additional mortality (Kuno 1981, Metz *et al.* 1983). Although there is limited evidence to support these hypotheses, the paradigm is widespread that reef fish larvae should disperse to develop offshore rather than near reefs.

Despite some benefits from the offshore dispersal of reef fish larvae, there are also disadvantages. For instance, it is necessary for larvae to return to a site suitable for settlement at the completion of their planktonic phase. The scale of most offshore dispersal makes active migration unlikely, but there is a variety of oceanographic processes that can transport reef fish larvae back to the nearshore environment (see review by Kingsford 1990). However, such processes are likely to be variable both in their presence and in their effectiveness. If larvae that are competent to settle are not transported back to shore, or if they are transported to an unsuitable habitat, then they are effectively lost.

These potential losses have led several authors to investigate an alternative strategy of reef fish larvae being retained near reefs during their planktonic phase. Brogan (1994a) suggested that such a distribution would have consequences on the mortality rate of larvae both before and after they become competent to settle. The presence of predators and increased competition for food may increase the precompetent larval mortality rate in the reef environment. However, once competent to settle, larvae near reefs are able to settle quickly, while offshore larvae may have to delay settlement until a suitable habitat is encountered, thereby risking further mortality.

Many reef fish species are pelagic spawners and, unless favourable hydrographic conditions prevail (Black *et al.* 1991, Black 1993), their eggs are passively dispersed by wind- and tide-induced currents. Pelagic eggs are generally smaller than demersal eggs and produce smaller larvae (3 to 5 mm) (Thresher 1984) with less developed sensory systems and swimming abilities (Blaxter 1986, Miller *et al.* 1988). The newly hatched larvae may undergo further passive dispersal before becoming functionally competent. Non-pelagic spawners (viviparous and demersal spawners) incubate their eggs on the reef and in many cases delay hatching or birth until the resulting larvae have reached a comparatively large size (5 to 10 mm) (Thresher 1984) with functional fins, eyes and guts (Barlow 1981, Hunter 1981, Thresher 1984). This combination of better swimming ability and more developed sensory systems may make retention more likely for non-pelagic spawners, particularly those species that hatch as large, well-developed larvae.

Several authors have found evidence of retention of reef fish larvae in temperate waters. On the Canadian west coast, the larvae from demersal eggs (Cottidae, Stichaeidae, Pholidae and Gobiesocidae) were dominant inshore and had a restricted alongshore distribution, favouring a rocky shoreline over sand (Marliave 1986). In contrast, larvae originating from pelagic eggs (Osmeridae, Bathylagidae, Gadidae, Pleuronectidae and Scorpaenidae) were more uniformly distributed both alongshore and offshore. Off southwestern Nova Scotia, the larvae from demersal eggs (Pholidae, Stichaeidae, Cottidae and Agonidae) dominated the inshore shallow-water environment, while densities of larvae originating from pelagic eggs (Gadidae and Pleuronectidae) were not correlated with bathymetry (Suthers & Frank 1991). The authors concluded that larvae from demersal eggs were more spatially persistent through the release of well-developed larvae from non-drifting eggs.

In the Gulf of California, Mexico, several families, including sandy bottom (Gobiidae) and reef fish (Bythitidae, Chaenopsidae, Gobiesocidae, Labrisomidae and Tripterygiidae), utilised the near-reef habitat throughout their development (Brogan 1994a). These families all spawned non-pelagic eggs and had well-developed hatchlings, but the larvae of other families, with similar spawning patterns (Balistidae, Blenniidae an Pomacentridae), were not retained. Off central New South Wales, Australia, larvae from taxa with demersal eggs (Gobiidae and Tripterygiidae) or that were viviparous (Clinidae) were more abundant close to shore (Gray 1993). However, some larvae that originated from pelagic eggs (Labridae and Sillaginidae) also predominated near shore. In northeastern New Zealand, the larvae from taxa that spawn demersal eggs (Tripterygiidae, Gobiesocidae, Acanthoclinidae, Eleotrididae and Gobiidae) were more abundant near reefs (Kingsford & Choat 1989). All larval size classes were present near reefs and these taxa were absent or rare farther offshore. However, the authors noted that the pelagic-demersal retention distinction was not consistent, as the distribution of several demersal spawning families (Bleniidae and Monacanthidae) was not influenced by the proximity of reefs.

Although several authors have identified the retention of reef fish larvae in temperate regions, many of these studies have been done on protected shorelines. Of interest is whether retention can still occur on a coastline exposed to large oceanic swells and storm events. In this chapter, I describe a study of larval fish distribution alongshore from a rocky reef environment on an exposed shoreline. The main questions addressed were:

1. Can reef fish larvae resist alongshore dispersal on an exposed coast?
2. Is larval retention restricted to taxa that have non-pelagic eggs?
3. Do fish larvae in the near-shore environment have a restricted vertical distribution?

4.2 METHODS

4.2.1 Study area

Sampling was done at four stations along the south coast of the Kaikoura Peninsula (Fig. 4.1). The stations were selected on the basis of their differing proximity to rocky reefs. The first three stations were all 50 m offshore from a fine shingle beach (5-10 mm particle diameter) but differed in their proximity to rocky reefs. The beach is very exposed to both southerly storms and the prevailing northeasterly winds. The resulting wave action, combined with the limestone

composition of the Peninsula, frequently results in heavy sediment loads in the coastal waters and a distinct milky inshore band. The Kowhai station (42° 25.144' S; 173° 38.405' E) was at a water depth of 9 m, and was 1 km from the nearest rocky reef. The Caves station (42° 24.978' S; 173° 39.543' E) was at a water depth of 9 m and was 300 m from the nearest rocky reef. The Racecourse station (42° 25.022' S; 173° 40.424' E) was at a water depth of 8 m and was 100 m from the nearest rocky reef. The Baxter's station (42° 25.899' S; 173° 40.886' E) was 50 m offshore from a rocky shoreline, at a water depth of 12 m and within South Bay. South Bay is surrounded by rocky reefs, but is very exposed to southerly storms.

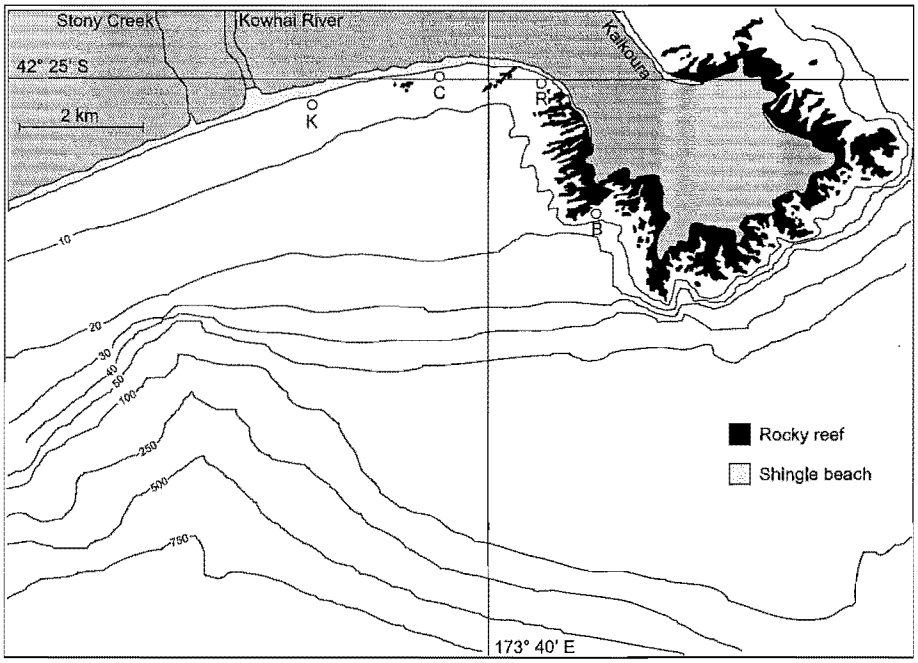

Figure 4.1. Map of the Kaikoura Peninsula on the northeast coast of the South Island. The four stations are shown (K: Kowhai; C: Caves; R: Racecourse and B: Baxter's). Bathymetry is in metres.

4.2.2 Sampling procedure

Ichthyoplankton surveys were done at the four stations on two occasions in late summer and on two occasions in mid-autumn (Table 4.1). Sampling was completed during daylight hours in the early morning. Logistical constraints required that two stations be sampled on each of two consecutive days. The stations were sampled in a random order. At each station, three replicate 15 minute tows were made at each of two depths (surface (0 m) and 3 m), using a plankton net with a 707 x 707 mm mouth (0.5 m^2) and 280 µm mesh. Samples from the two depths were taken in alternate order, with the initial depth chosen randomly. The plankton net was a box-pyramid design with a filtration efficiency of 1:11. A General Oceanics flowmeter (Model 2030R) was fitted within the mouth of the net (0.33 of the net width) to determine the volume of water filtered per tow. The net was rigged to be towed alongside a 6 m boat to avoid disturbance caused by the wake. The top of the net frame was suspended from a gantry so that it sampled at a fixed depth. A 25 kg Scripps depressor was suspended from the lower edge of the frame to keep the net mouth vertical in the water column. During surface samples, the upper edge of the mouth of the net was held at approximately 10 cm above the surface of the water (Fig. 2.8).

The flowmeter was submerged at all times. For 3 m samples, the upper edge of the mouth of the net was held at 3 m below the surface of the water. The net was towed with a four-point bridle that joined above the level of the mouth of the net to avoid disturbance caused by the wire strops. The net was towed at ca. 1.3 ms^{-1} and filtered an average of 524 m^3 of water per replicate.

Table 4.1. Sampling dates and season.

Sampling Dates	Season
28th - 29th January 1997	Summer
18th - 19th February 1997	
2nd - 3rd April 1997	Autumn
16th - 17th April 1997	

After the completion of each sample, the plankton net was washed thoroughly with pumped seawater and the sample was fixed in buffered 10% formalin in seawater. All larval fish were removed from the samples using a dissection microscope, identified to the lowest possible taxonomic level, counted and stored in buffered 2% formalin in freshwater. Counts were standardised to the number of fish per 500 m^3. Clupeid, retropinnid and galaxiid larvae could not be identified beyond the family or genus level because of the similarities of larvae from individual species and the presence of adults from several species of each of these families in the study area. Small scorpaenids, morids and tripterygiids could also not be identified below the family or genus level. All fish (except those that were badly damaged) were measured to the nearest 0.5 mm by placing them on a graduated slide. Notochord length was measured for preflexion and flexion larvae, and standard length was measured for postflexion larvae.

4.2.3 Analysis

Two types of data were collected during this study. The ichthyoplankton samples contained a wide range of taxa, allowing tests on both the temporal and spatial distribution of individual taxa and species richness. Because all undamaged fish larvae were measured, the size of larvae could also be compared both spatially and temporally.

To compare the abundances of the commonly occurring taxa (> 1% of the total number caught), all taxa and species richness, mixed model ANOVAs were used with season (summer and autumn), occasion within season (treated as random), station (treated as random) and depth (0 and 3 m) as factors. Prior to ANOVA, the data for each taxon were tested for homogeneity of variances using Cochran's test, and all data became homogeneous when log (x+1) transformed. Tukey's Honest Significant Difference (HSD) tests were used for *post hoc* comparison of means.

The analysis of size data was complicated by missing cells in the data matrix. These missing cells arose when no larvae from a particular taxon were collected in a sample. For each commonly occurring taxon, ANOVA was used, where possible, to compare the size of larvae

at different stations, different depths or on different occasions. Tukey's HSD tests for unequal n were used for *post hoc* comparison of means.

Correlation analysis was used to investigate any similarities in the distribution of commonly occurring taxa. The resulting correlation matrices were corrected for multiple comparisons by using an adjusted α level (Ezekiel 1945). The corrected α level was derived from the equation

$$\alpha_{corrected} = \frac{0.05}{no.\ of\ correlations}$$

Principal components analysis (PCA) of abundance was then used to display any relationships in the taxonomic composition of the samples. Data were log (x+1) transformed prior to analysis.

4.3 RESULTS

In total, the 96 samples collected 5,625 larval and pelagic juvenile fish from 20 families (Table 4.2). Thirty taxa were identified, including seven that contained more than one species (identifiable to the family or genus level). The damaged category contained larvae that were unidentifiable as a result damage during capture. The four most abundant taxa accounted for ca. 67% of the total catch. These were Retropinnidae (23.6%), *Trachelochismus melobesia* (16.3%), unidentified Scorpaenidae (15.0%) and *Grahamichthys radiata* (11.6%). Eighteen taxa each comprised < 1% of the total number of larvae collected. Of the twelve more common taxa, only *Sprattus* spp. and galaxiid larvae occurred in less than 20% of samples. Instead of occurring in very low numbers throughout all samples, most of the less common taxa occurred in only a few samples. Six taxa occurred in only a single sample (1.0% occurrence).

Table 4.2. Composition and size range of fish larvae in the samples. Total abundance (n), percentage of total catch when adjusted for volume (%), percentage occurrence in the 96 samples (% Occ), the number measured and their mean, minimum and maximum size (mm) are given for each taxon.

Family	Taxon	n	%	% Occ	Measured	Mean	Min	Max
Clupeidae	*Sprattus* spp.	420	8.9	18	391	6.9	2	36
Gonorynchidae	*Gonorynchus gonorynchus*	1	0.0	1	1	109.0	109	109
Retropinnidae	Retropinnidae	1798	23.6	64	1743	23.2	4	57
Galaxiidae	Galaxiidae	59	1.3	3	53	9.5	8	11
Myctophidae	*Gymnoscopelus piabilis*	1	0.0	1	1	6.0	6	6
	Symbolophorus boops	47	0.8	16	47	5.5	4	16
Moridae	Moridae	22	0.7	6	22	3.4	2	4
Gobiesocidae	*Diplocrepis puniceus*	21	0.4	10	21	4.6	2	7.5
	Trachelochismus melobesia	787	16.3	31	779	4.2	2.5	8
Trachichthyidae	*Paratrachichthys trailli*	3	0.1	3	3	3.8	3.5	4.5
Syngnathidae	*Hippocampus abdominalis*	5	0.1	5	5	33.0	13	107
	Lissocampus filum	7	0.1	6	7	7.1	5.5	9
Scorpaenidae	Unidentified Scorpaenidae	699	15.0	70	699	2.4	1.5	6
	Scorpaena papillosus	1	0.0	1	1	16.0	16	16
Acanthoclinidae	*Acanthoclinus fuscus*	1	0.0	1	1	4.0	4	4
Mugilidae	*Aldrichetta forsteri*	167	2.2	20	167	26.6	5	37
Labridae	*Notolabrus celidotus*	1	0.0	1	1	4.5	4.5	4.5
Uranoscopidae	*Genyagnus monopterygius*	1	0.0	1	1	13.0	13	13
Tripterygiidae	Unidentified Tripterygiidae	172	2.9	33	165	11.4	2.5	22.5
	Forsterygion spp.	225	4.4	33	221	5.2	2	10
	Forsterygion varium	122	1.7	29	121	20.2	10.5	25
	Gilloblennius tripennis	24	0.4	13	22	6.0	3	16
	Grahamina capito	99	1.7	25	98	12.3	6.5	18.5
	Ruanoho decemdigitatus	39	0.6	14	39	4.4	3	14.5
Eleotrididae	*Grahamichthys radiata*	555	11.6	20	542	7.1	2	25
Gobiidae	*Gobiopsis atrata*	15	0.3	6	15	3.8	2	9
Centrolophidae	*Seriolella punctata*	3	0.1	3	3	3.3	2.5	4.5
Pleuronectidae	*Pelotretis flavilatus*	4	0.1	4	4	5.1	4.5	5.5
	Rhombosolea plebeia	301	6.1	45	301	4.9	2	17
Monacanthidae	*Parika scaber*	3	0.0	2	3	19.8	15.5	23.5
	Damaged	22	0.4	13	0	-	-	-
Total		5625			5477	12.1	1.5	109

There was considerable variation among the twelve common taxa in the habitat occupied by adults and in their mode of spawning (Table 4.3). Most of the common taxa hatched from demersal eggs, but viviparous taxa and larvae from pelagic eggs were also present. Most of the larvae were from taxa whose adults occupied rocky reef habitats, but inshore pelagic taxa, anadramous freshwater taxa (retropinnids) and amphidromous freshwater taxa (galaxiids) were also common.

Table 4.3. Life history characteristics of the twelve common taxa collected in the samples. The habitats occupied by adult fish and their mode of spawning are indicated. Habitats: IP, inshore pelagic; F, freshwater and estuaries; R, rocky reef; S, sand. Mode of spawning: P, pelagic eggs; FD, freshwater demersal eggs then marine larvae; D, demersal eggs; V, viviparous. Sources of information are shown.

Family	Taxon	Adult	Spawning	Source
Clupeidae	*Sprattus* spp.	IP	P	Ayling & Cox 1987
Retropinnidae	Retropinnidae	IP, F	FD	McDowall 1990
Galaxiidae	Galaxiidae	F	FD	McDowall 1990
Gobiesocidae	*Trachelochismus melobesia*	R	D	Ayling & Cox 1987
Scorpaenidae	Scorpaenidae	R	P, V	Ayling & Cox 1987
Mugilidae	*Aldrichetta forsteri*	IP, F	P	McDowall 1990
Tripterygiidae	Unidentified Tripterygiidae	R	D	Crossland 1981
	Forsterygion spp.	R	D	Crossland 1981
	Forsterygion varium	R	D	Crossland 1981
	Grahamina capito	R	D	Crossland 1981
Eleotrididae	*Grahamichthys radiata*	R, S	D	Crossland 1981
Pleuronectidae	*Rhombosolea plebeia*	S, F	P	Ayling & Cox 1987

Overall, 5,477 larval fish (97% of all larvae collected) were measured. They ranged from a 1.5 mm scorpaenid to a 109 mm *Gonorynchus gonorynchus*. Within the twelve most common taxa, the mean larval size ranged from 2.4 mm for unidentified scorpaenids to 26.6 mm for *A. forsteri*. The overall mean size of larval fish captured was 12.1 mm.

The abundance of the twelve common taxa varied temporally (among sampling occasions) and spatially (either among stations or between depths) (Table 4.4). In most taxa, the 3-way interaction term was significant. However, in many instances this and the other interaction terms accounted for relatively little of the total variation in abundance. For all taxa combined, taxonomic richness and the twelve common taxa, Tukey HSD tests were used to discern consistent spatial and temporal patterns in the densities of fish larvae.

Table 4.4. Summary results from ANOVA of the abundance of all taxa combined, taxonomic richness and the twelve common taxa with time (x4), station (x4) and depth (x2) as factors. Significance is indicated (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$). The variance has been partitioned (%) for each factor and the interaction terms. ANOVA could not be done on Galaxiidae larvae because of their limited occurrence.

	Occasion		Station		Season x Station		Occasion x Station		Occasion x Depth		Station x Depth		Season x Station x Depth		Occasion x Station x Depth		Res
df	2,6		3,6		3,6		6,64		2,6		3,6		3,6		6,64		64
	F	%	F	%	F	%	F	%	F	%	F	%	F	%	F	%	%
All taxa	2.3	13	0.1	1	0.9	8	18.7***	17	6.1*	16	2.5	10	2.7	11	8.7***	8	17
Number of Taxa	2.1	13	2.1	21	0.1	1	9.1***	19	0.4	2	1.7	10	0.5	3	5.8***	12	19
Sprattus spp.	0.7	7	0.3	5	0.4	6	21.1***	28	0.8	4	0.2	28	0.3	3	13.2***	18	28
Retropinnidae	1.4	11	0.7	9	1.3	16	42.5***	24	3.5	4	5.1*		1.0	2	5.8***	3	24
Galaxiidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
T. melobesia	0.5	2	4.2	19	4.3	20	7.0***	9	0.6	1	13.2**	20	12.7**	19	2.3*	3	9
Scorpaenidae	12.6**	44	2.8	15	1.3	7	14.6***	11	24.6**	5	10.4**	3	17.6**	5	0.8	1	11
A. forsteri	1.6	7	1.0	7	2.1	15	1.4	14	1.6	7	1.0	7	2.1	15	1.4	14	14
Tripterygiidae	3.6	15	2.2	14	0.8	5	7.0***	12	3.9	11	4.1	17	1.4	6	4.7***	8	12
Forsterygion spp.	5.5*	10	6.4*	17	5.6*	15	4.2***	5	0.2	0	7.5*	20	8.2*	22	4.2***	5	5
F. varium	0.9	8	0.3	3	0.0	0	10.4***	26	4.3	14	2.3	11	0.7	4	3.8***	10	26
G. capito	3.2	8	9.4*	35	8.9*	33	4.5***	8	1.7	1	3.7	2	7.6*	5	0.7	1	8
G. radiata	0.0	0	0.1	2	0.1	2	109.6***	31	0.0	0	0.1	2	0.1	2	109.6***	31	31
R. plebeia	1.4	13	0.5	7	0.6	9	35.1***	29	3.2	5	0.9	2	0.6	1	5.5***	5	29

The total catch of fish larvae was evenly distributed among the four stations when all four occasions were combined (K 25%, C 21%, R 31%, B 22%) (Fig. 4.2). However, there was considerable variation among occasions, with large numbers of larvae being caught at different stations and different depths on different days. Overall, most fish larvae (ca. 66%) were found at 3 m, but this was not consistent among occasions. Most fish larvae (ca. 73%) were found in summer.

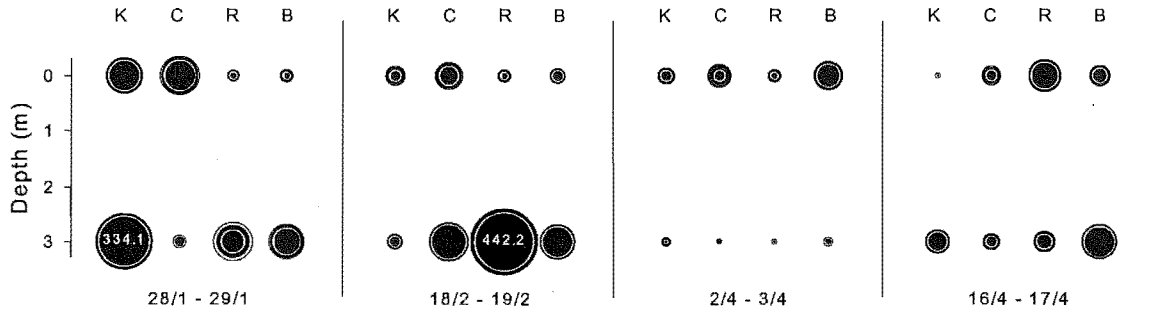

Figure 4.2. The mean abundance ± SE per 500 m^3 of larvae from all taxa found at two depths (0 and 3 m), at four stations (Kowhai, Caves, Racecourse and Baxter's) on four occasions. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area (white text) is proportional to the mean abundance.

The summer samples contained a larger mean number of taxa than the autumn samples, and overall, the 3 m samples contained more taxa than the 0 m samples (Fig. 4.3). The highest taxonomic richness in a sample was 11. This was recorded in several 3 m samples at the Baxter's station in summer. On most occasions, the samples from both depths at the Baxter's station contained the largest mean number of taxa.

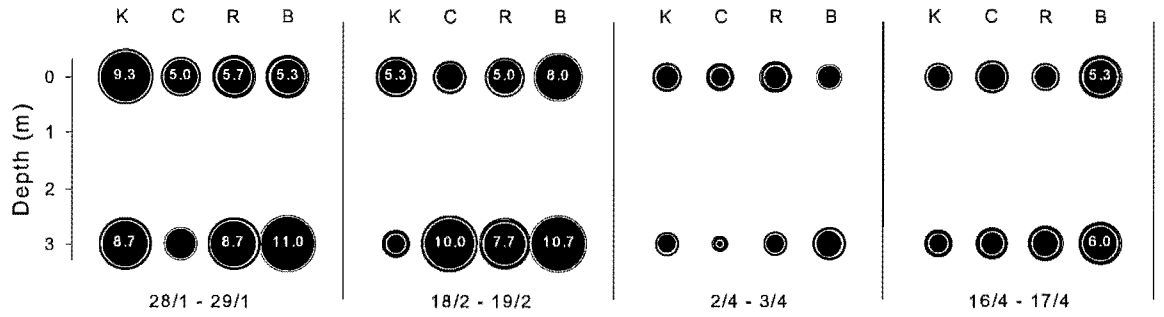

Figure 4.3. The taxonomic richness ± SE per 500 m^3 of at two depths (0 and 3 m), at four stations (Kowhai, Caves, Racecourse and Baxter's) on four occasions. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area (white text) is proportional to the mean abundance.

Most of the *Sprattus* spp. larvae (ca. 99%) were found at 3 m (Fig. 4.4). However, there was no consistent pattern among the stations in the abundance of larvae. The few larvae that were found at 0 m were generally larger than those at 3 m.

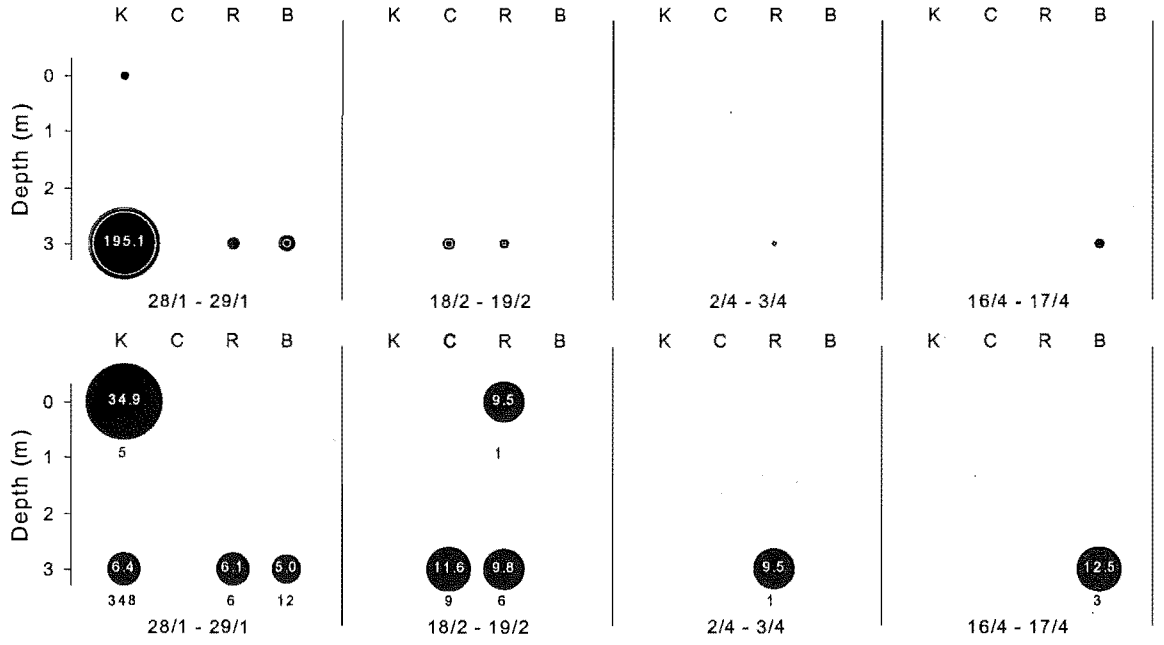

Figure 4.4. The mean abundance ± SE per 500 m^3 (upper graph) and mean size (mm) (lower graph) of *Sprattus* spp. larvae found at two depths (0 and 3 m), at four stations (Kowhai, Caves, Racecourse and Baxter's) on four occasions. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area (white text) is proportional to the mean abundance and mean size. The number of larvae that were measured is given under each data point in the lower graph.

Most of the retropinnid larvae (ca. 96%) were found at 0 m (Fig. 4.5). However, there was no consistent pattern among the stations in the abundance of larvae. In mid-April, the larvae collected at the Caves station were larger on average than those at the Kowhai or Racecourse stations ($F_{2,1434}$ = 41.31, $p < 0.001$). However, there was no difference among the mean sizes of larvae collected at these three stations on the previous three occasions (Tukey HSD, $p > 0.05$). The mean size of larvae collected at these three stations increased between the summer samples and the autumn samples ($F_{3,1434}$ = 59.15, $p < 0.001$).

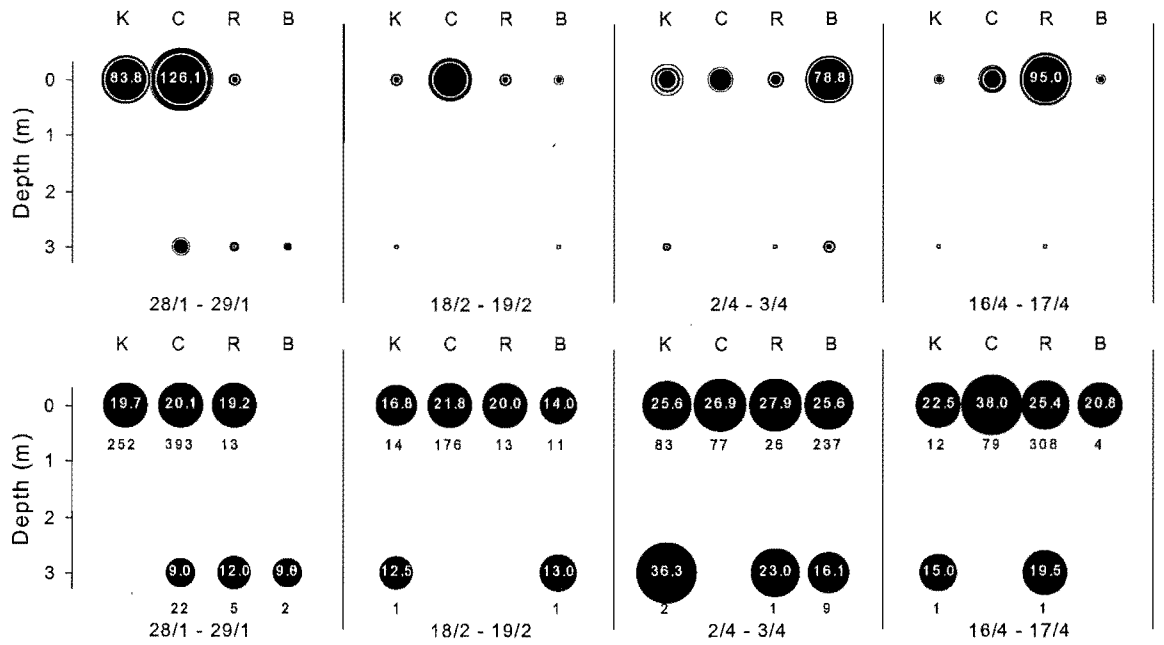

Figure 4.5. The mean abundance ± SE per 500 m^3 (upper graph) and mean size (mm) (lower graph) of retropinnid larvae found at two depths (0 and 3 m), at four stations (Kowhai, Caves, Racecourse and Baxter's) on four occasions. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area (white text) is proportional to the mean abundance and mean size. The number of larvae that were measured is given under each data point in the lower graph.

All of the galaxiid larvae were found at 0 m at the Kowhai station in mid-February (Fig. 4.6). They were collected evenly across the three replicates, and their mean size was 9.5 mm.

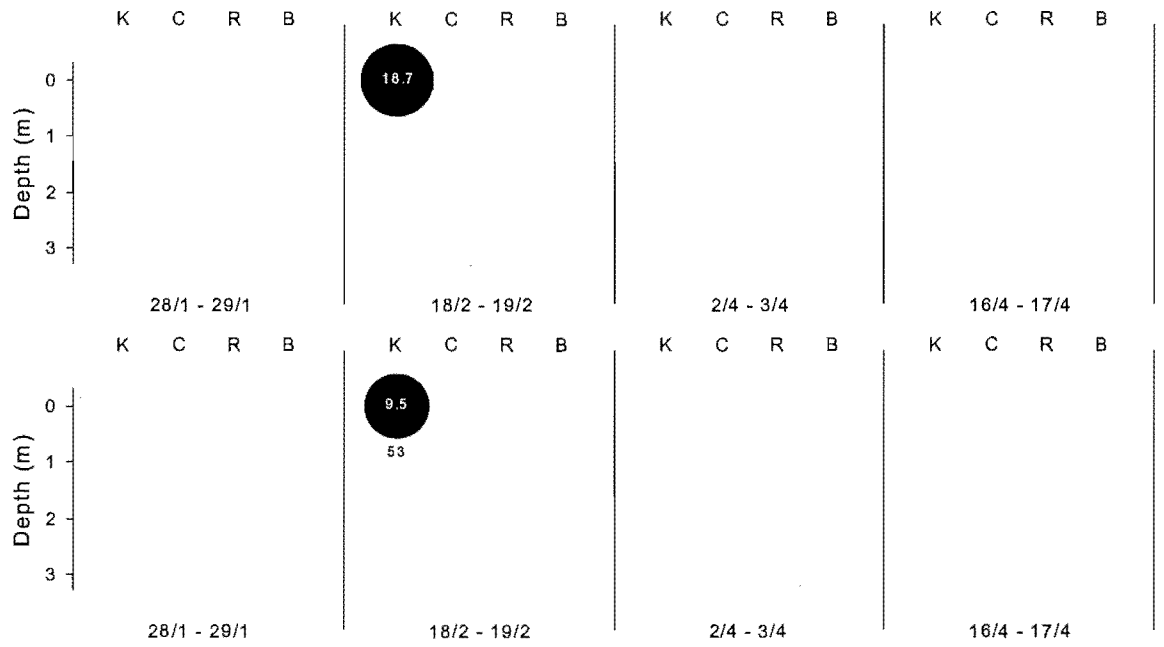

Figure 4.6. The mean abundance ± SE per 500 m^3 (upper graph) and mean size (mm) (lower graph) of galaxiid larvae found at two depths (0 and 3 m), at four stations (Kowhai, Caves, Racecourse and Baxter's) on four occasions. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area (white text) is proportional to the mean abundance and mean size. The number of larvae that were measured is given under each data point in the lower graph.

Most of the *T. melobesia* larvae (ca. 99%) were found at 3 m, and most of these were in summer samples (Fig. 4.7). *T. melobesia* larvae were more abundant at the Racecourse station on both occasions in summer. However, on both of these occasions the larvae at the Kowhai and Caves stations were larger on average than those at the Racecourse or Baxter's stations ($F_{3,757}$ = 158.26, $p < 0.001$).

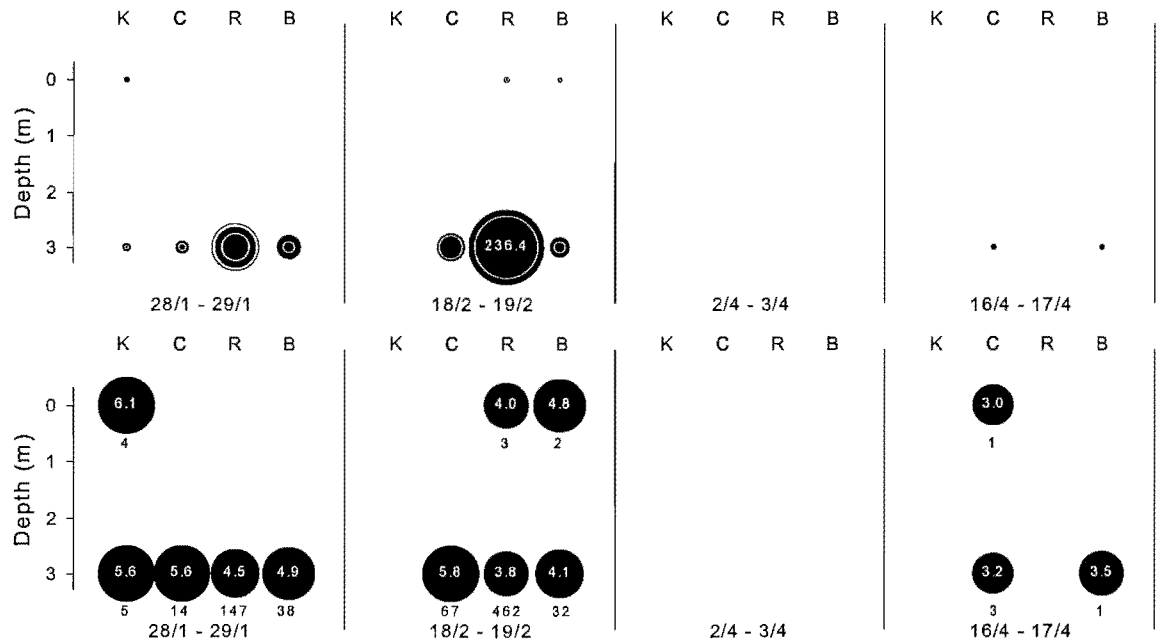

Figure 4.7. The mean abundance ± SE per 500 m^3 (upper graph) and mean size (mm) (lower graph) of *Trachelochismus melobesia* larvae found at two depths (0 and 3 m), at four stations (Kowhai, Caves, Racecourse and Baxter's) on four occasions. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area (white text) is proportional to the mean abundance and mean size. The number of larvae that were measured is given under each data point in the lower graph.

Most of the unidentified scorpaenid larvae (ca. 83%) were found at 3 m (Fig. 4.8). However, there was no consistent pattern among the stations in the abundance of larvae. There was no difference between the mean sizes of larvae at the two depths in mid-February or mid-April ($F_{1,608} = 0.90$, $p = 0.34$), and no difference among the stations in mid-February (Tukey HSD, $p > 0.05$). However, by mid-April the larvae at the Baxter's station were larger on average than those at the other three stations ($F_{3,608} = 6.98$, $p < 0.001$).

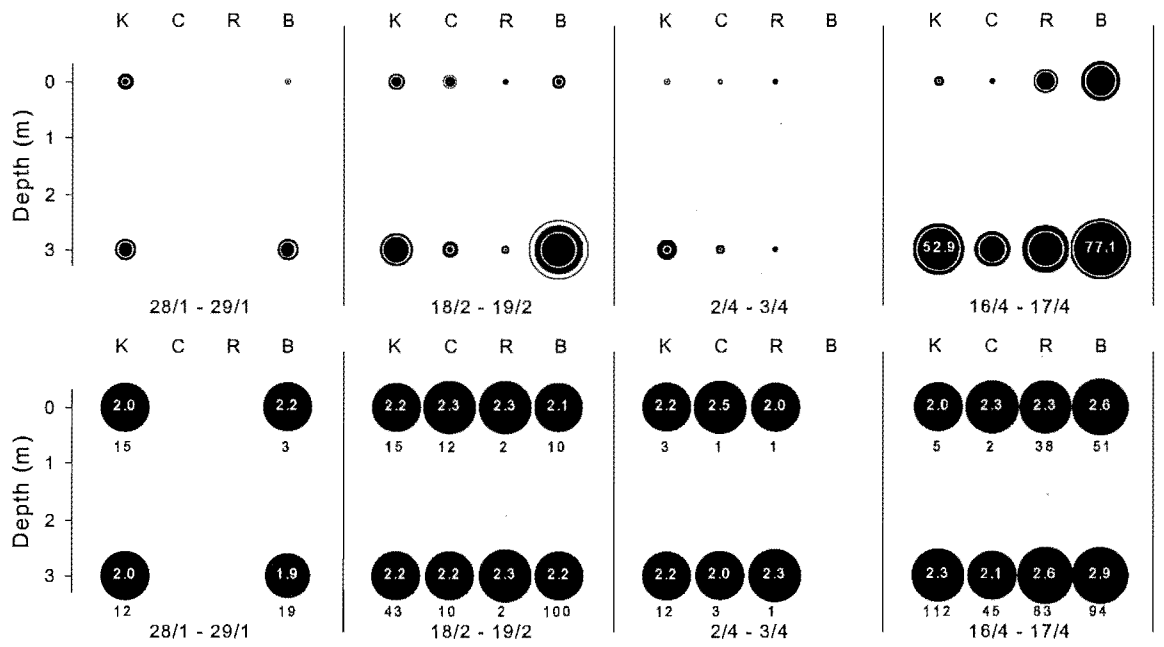

Figure 4.8. The mean abundance ± SE per 500 m^3 (upper graph) and mean size (mm) (lower graph) of unidentified scorpaenid larvae found at two depths (0 and 3 m), at four stations (Kowhai, Caves, Racecourse and Baxter's) on four occasions. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area (white text) is proportional to the mean abundance and mean size. The number of larvae that were measured is given under each data point in the lower graph.

All of the *A. forsteri* larvae were found at 0 m, and 94% of these were found in autumn (Fig. 4.9). The *A. forsteri* larvae were most abundant at the Caves station on both occasions in autumn. However, there was no difference among the mean sizes of larvae collected at the four stations in early April ($F_{3,73}$ = 10.38, p = 0.12).

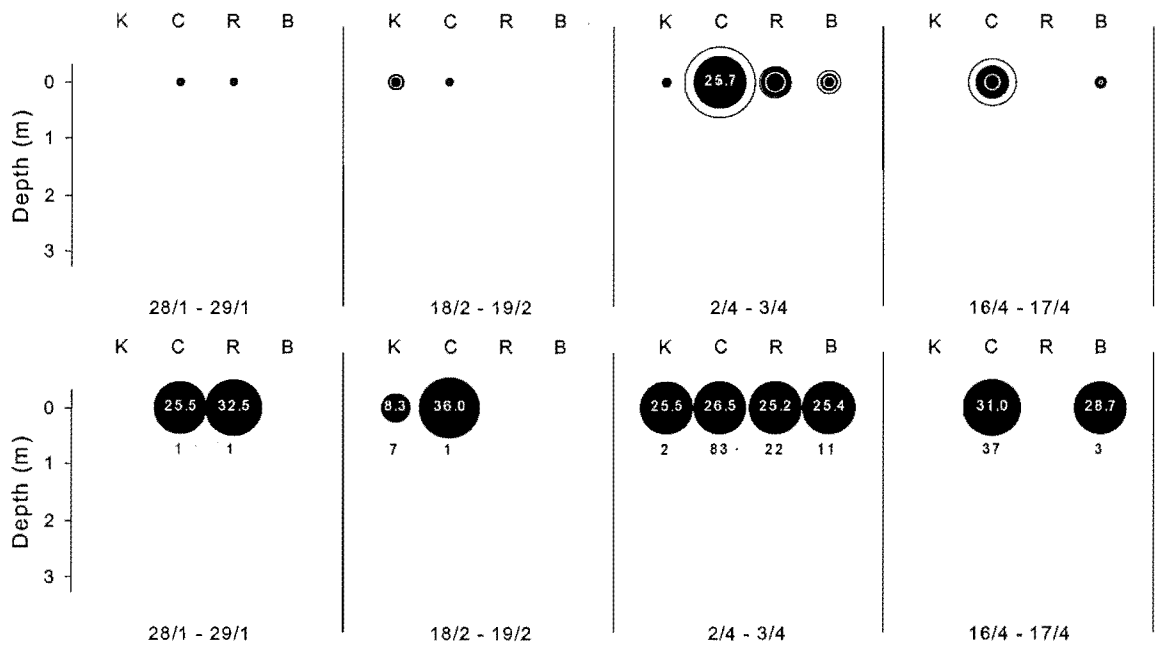

Figure 4.9. The mean abundance ± SE per 500 m^3 (upper graph) and mean size (mm) (lower graph) of *Aldrichetta forsteri* larvae found at two depths (0 and 3 m), at four stations (Kowhai, Caves, Racecourse and Baxter's) on four occasions. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area (white text) is proportional to the mean abundance and mean size. The number of larvae that were measured is given under each data point in the lower graph.

Most of the unidentified tripterygiid larvae (ca. 95%) were found in summer (Fig. 4.10). The larvae were consistently abundant at 3 m at the Baxter's station, but also occurred in relatively large numbers at 0 m at other stations. The larvae found at 0 m in late January were larger on average at the Kowhai and Caves stations than those at the Racecourse and Baxter's stations ($F_{3,73} = 10.38$, $p < 0.001$).

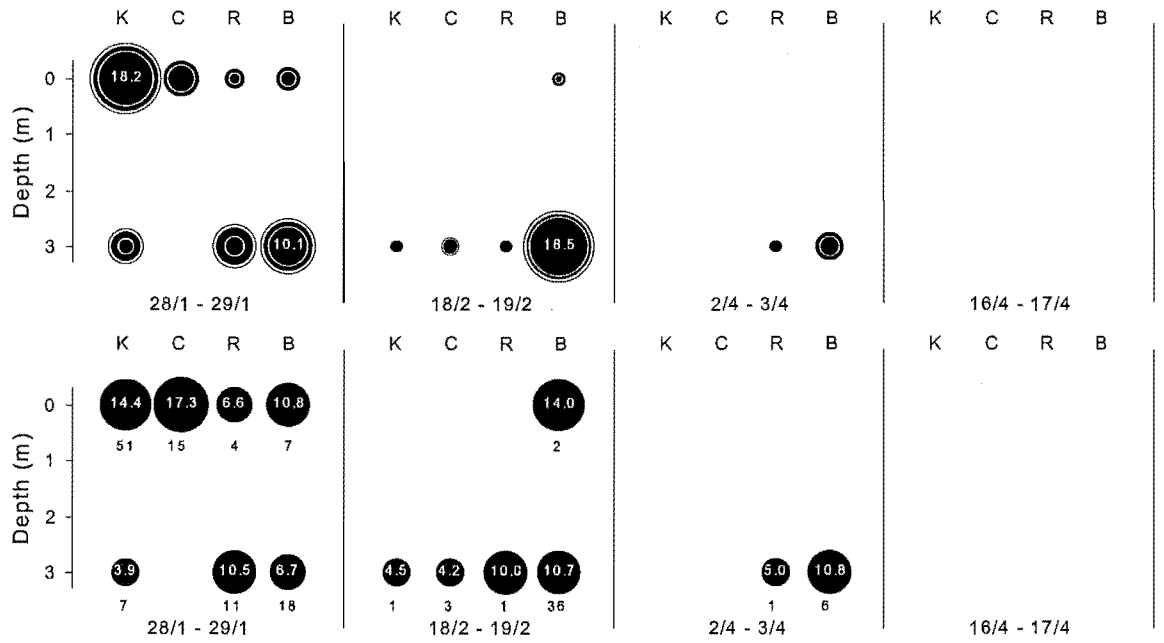

Figure 4.10. The mean abundance ± SE per 500 m^3 (upper graph) and mean size (mm) (lower graph) of unidentified tripterygiid larvae found at two depths (0 and 3 m), at four stations (Kowhai, Caves, Racecourse and Baxter's) on four occasions. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area (white text) is proportional to the mean abundance and mean size. The number of larvae that were measured is given under each data point in the lower graph.

All but one of the *Forsterygion* spp. larvae were found in summer (Fig. 4.11). Significantly more larvae were found at 3 m at the Racecourse and Baxter's stations than at any other station or depth (Tukey HSD, $p < 0.001$). The *Forsterygion* spp. larvae found at 3 m at the Baxter's station were larger on average than those at the Racecourse station ($F_{1,177} = 59.32$, $p < 0.001$).

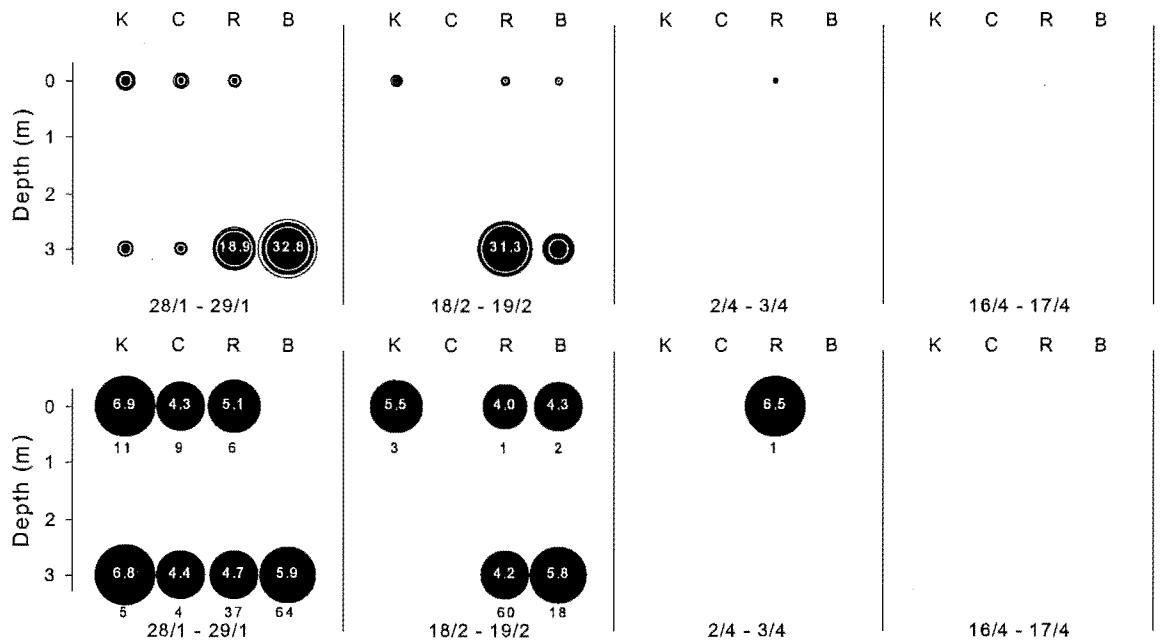

Figure 4.11. The mean abundance ± SE per 500 m^3 (upper graph) and mean size (mm) (lower graph) of *Forsterygion* spp. larvae found at two depths (0 and 3 m), at four stations (Kowhai, Caves, Racecourse and Baxter's) on four occasions. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area (white text) is proportional to the mean abundance and mean size. The number of larvae that were measured is given under each data point in the lower graph.

Most of the *F. varium* larvae (ca. 95%) were found in summer (Fig. 4.12). However, there were no consistent patterns among the stations or between the depths in the abundance of *F. varium* larvae. The mean size of larvae caught at 0 m in late January did not differ between the stations ($F_{2,84}$ = 0.06, p = 0.94).

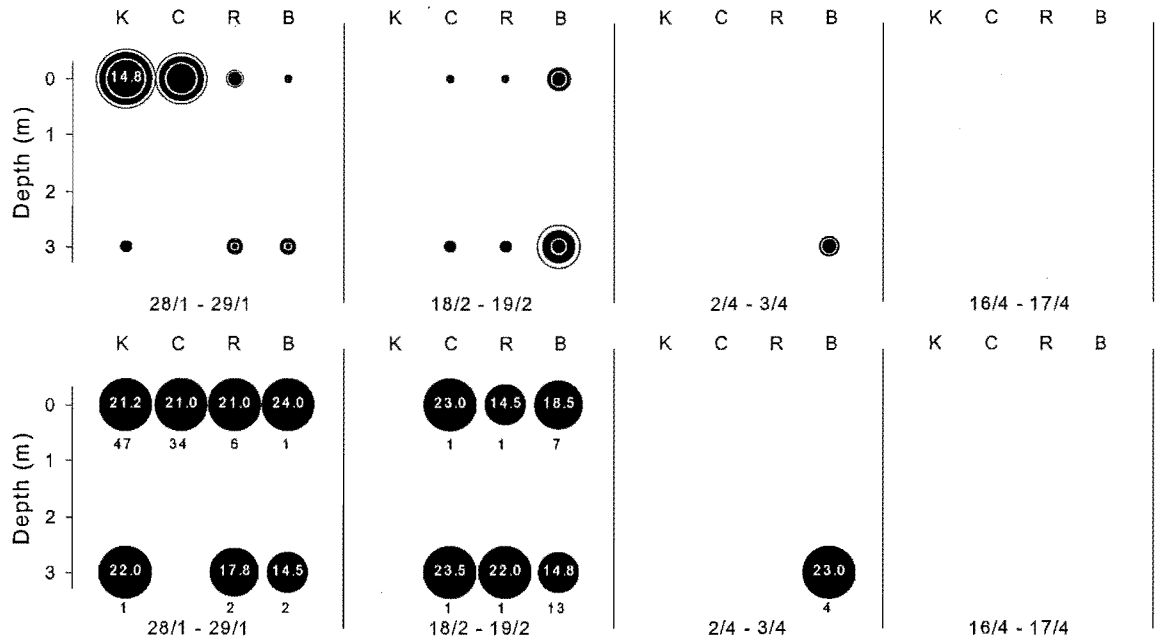

Figure 4.12. The mean abundance ± SE per 500 m^3 (upper graph) and mean size (mm) (lower graph) of *Forsterygion varium* larvae found at two depths (0 and 3 m), at four stations (Kowhai, Caves, Racecourse and Baxter's) on four occasions. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area (white text) is proportional to the mean abundance and mean size. The number of larvae that were measured is given under each data point in the lower graph.

Most of the *G. capito* larvae (ca. 98%) were found in summer (Fig. 4.13). *G. capito* larvae were more abundant at the Baxter's station than at the other three stations at both depths in summer (Tukey HSD, $p < 0.001$). There were few patterns in the mean size of *G. capito* larvae in the samples, but on most occasions when larvae were caught at both depths at the same station, the deeper samples contained smaller larvae.

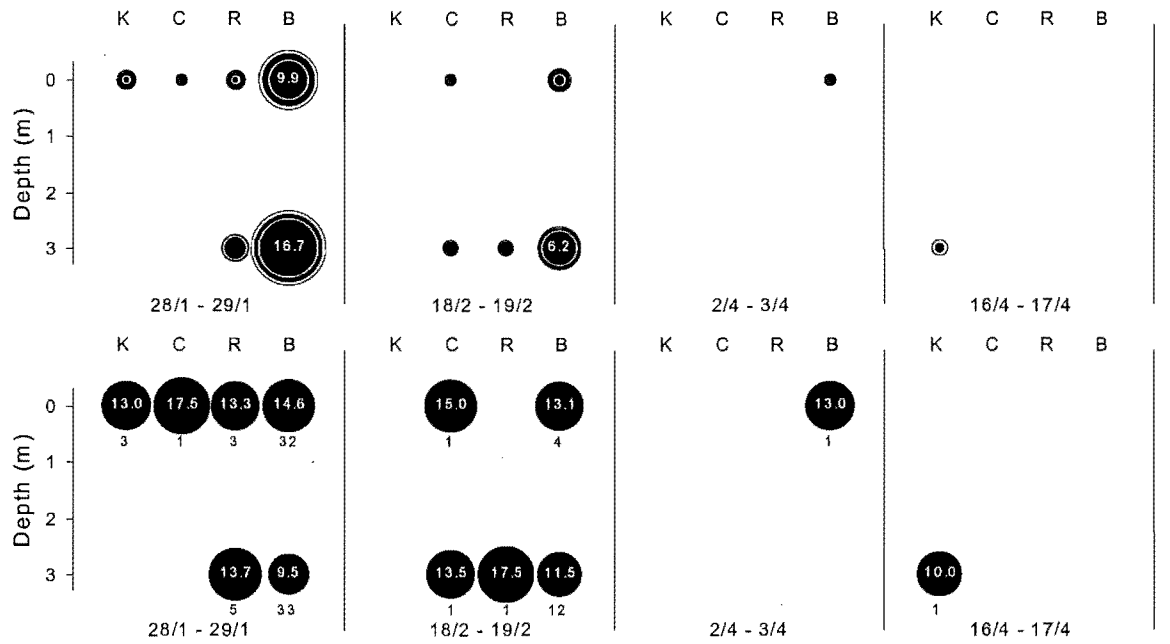

Figure 4.13. The mean abundance ± SE per 500 m^3 (upper graph) and mean size (mm) (lower graph) of *Grahamina capito* larvae found at two depths (0 and 3 m), at four stations (Kowhai, Caves, Racecourse and Baxter's) on four occasions. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area (white text) is proportional to the mean abundance and mean size. The number of larvae that were measured is given under each data point in the lower graph.

All of the *G. radiata* larvae were found at 3 m, and 99% of these were found in summer (Fig. 4.14). Larvae were found at all four stations during summer, but were never abundant at the Baxter's station. The mean size of *G. radiata* larvae was very similar between stations in late January, but by mid-February most larvae had increased in size considerably, and larvae at the Caves station were larger on average than those at the Racecourse station.

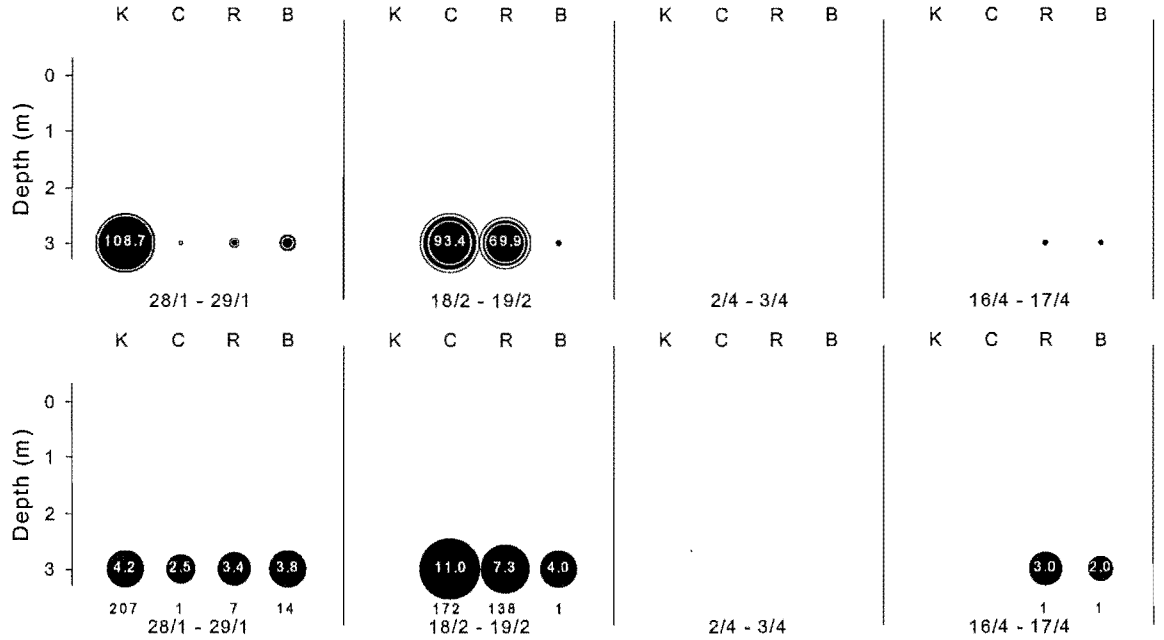

Figure 4.14. The mean abundance ± SE per 500 m^3 (upper graph) and mean size (mm) (lower graph) of *Grahamichthys radiata* larvae found at two depths (0 and 3 m), at four stations (Kowhai, Caves, Racecourse and Baxter's) on four occasions. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area (white text) is proportional to the mean abundance and mean size. The number of larvae that were measured is given under each data point in the lower graph.

Most of the *R. plebeia* larvae (ca. 63%) were found at 3 m at the Racecourse station in mid-February (Fig. 4.15). Other than this single pulse, the abundance of *R. plebeia* was comparatively even between depths and between stations. Very few larvae were found in early April. The mean size of *R. plebeia* larvae was very similar between the two depths and the four stations on any one occasion, but, as would be expected, increased between the first and last sampling occasion as the larvae developed.

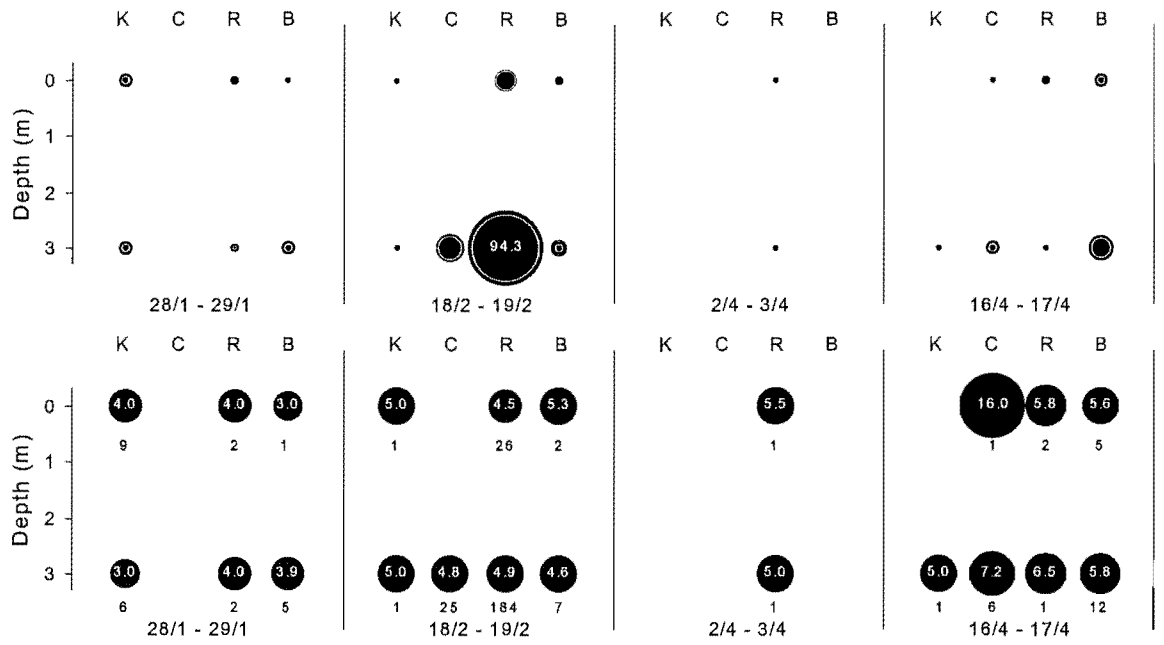

Figure 4.15. The mean abundance ± SE per 500 m^3 (upper graph) and mean size (mm) (lower graph) of *Rhombosolea plebeia* larvae found at two depths (0 and 3 m), at four stations (Kowhai, Caves, Racecourse and Baxter's) on four occasions. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area (white text) is proportional to the mean abundance and mean size. The number of larvae that were measured is given under each data point in the lower graph.

There are marked differences among the size-frequency distributions of the combined tripterygiids at the four stations (Fig. 4.16). The Kowhai samples contained a large size range of larvae, with a high proportion of larvae >20 mm (these were mainly *F. varium*). The Caves samples had a bimodal size-frequency distribution, with peaks at ca. 4 mm and 20 mm. Again, the larger tripterygiid larvae were predominately *F. varium*. The samples from both the Racecourse and Baxter's stations contained a very small proportion of large (>20 mm) tripterygiid larvae.

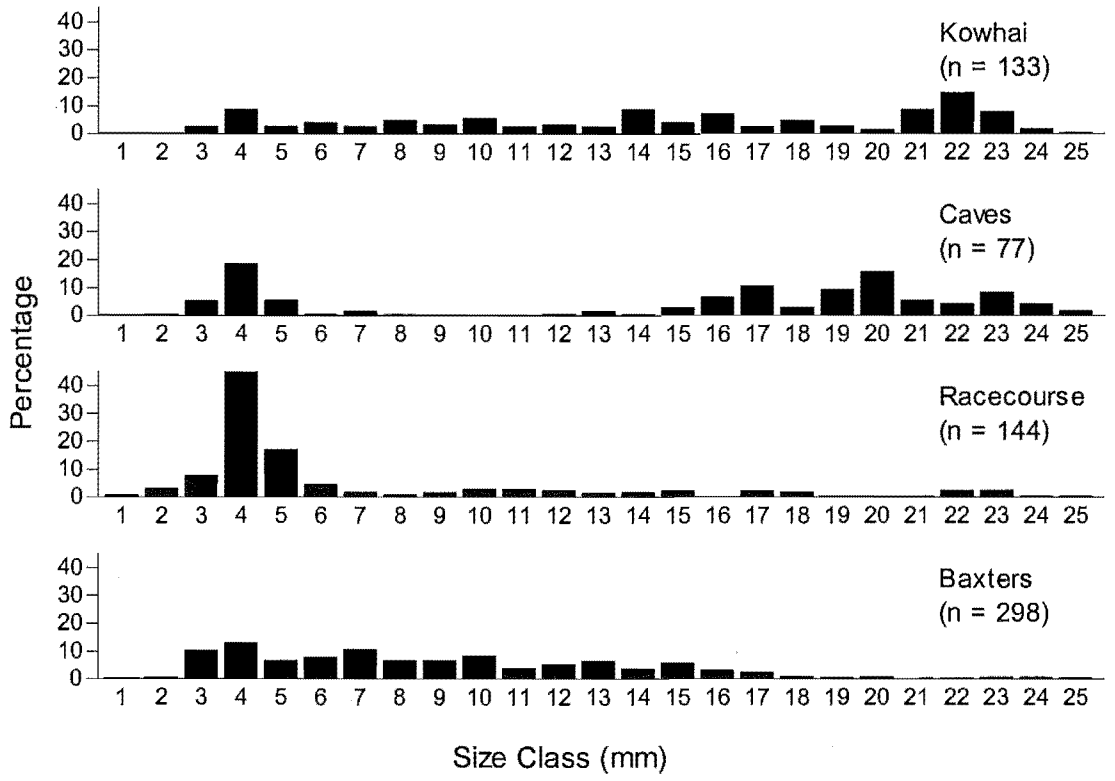

Figure 4.16. Size-frequency (%) distributions of all tripterygiid larvae collected at the four stations on all four occasions. Sizes have been rounded down to the nearest mm (n = the number of larvae that were measured at each station).

The abundances of many of the common taxa were positively correlated (Table 4.5), while retropinnid larvae were negatively correlated with several taxa. In examining the overall similarity of the samples, there were discrete clusters identified from a PCA. The first two components accounted for 51.2% of the variation in the data set. The PCA bi-plot can be interpreted by drawing a line through each taxon point and the origin (0,0). This line is then the imaginary axis for that taxon. When samples are projected onto this axis, those whose projection point is closest to the taxon point contained the highest abundance of that particular taxon. Similarly, the projection points of other taxa onto the imaginary axis will yield a ranking of correlations with the taxon that forms the imaginary axis. In this ranking, the origin indicates zero correlation.

Table 4.5. Pearson correlation coefficients for twelve common taxa using their abundance in 96 samples. Significant correlations are shown in bold. α level has been corrected for multiple comparisons: ($\alpha = \frac{0.05}{66} = 0.00076$, $r_{0.00076(2),94} = 0.341$).

	Retropinnidae	Galaxiidae	*Trachelochismus melobesia*	Scorpaenidae	*Aldrichetta forsteri*	Tripterygiidae	*Forsterygion* spp.	*Forsterygion varium*	*Grahamina capito*	*Grahamichthys radiata*	*Rhombosolea plebeia*
Sprattus spp.	-0.277	-0.067	**0.364**	0.101	-0.150	0.328	**0.357**	0.087	0.146	**0.759**	**0.366**
Retropinnidae		0.007	-0.328	**-0.390**	0.328	-0.020	-0.140	0.253	-0.210	**-0.375**	**-0.393**
Galaxiidae			-0.098	0.033	0.202	-0.110	-0.016	-0.095	-0.089	-0.075	-0.087
Trachelochismus melobesia				-0.058	-0.215	**0.364**	**0.760**	0.151	**0.365**	**0.704**	**0.663**
Scorpaenidae					-0.209	0.012	-0.080	-0.138	0.072	0.020	0.219
Aldrichetta forsteri						-0.227	-0.170	-0.166	-0.192	-0.168	-0.187
Tripterygiidae							**0.571**	**0.726**	**0.621**	0.237	0.132
Forsterygion spp.								**0.358**	**0.527**	**0.482**	**0.450**
Forsterygion varium									0.326	-0.009	0.056
Grahamina capito										0.132	0.105
Grahamichthys radiata											**0.623**

Retropinnids (Retro) and unidentified scorpaenids (Scorp) are separated from the other ten taxa on the PCA bi-plot, indicating that they have a markedly different temporal or spatial distribution (Fig. 4.17). Retropinnid and scorpaenid larvae were common in both the summer and autumn samples. Retropinnid larvae were primarily restricted to the 0 m samples, but scorpaenid larvae were much more abundant in the 3 m samples. All of the other common taxa, except *A. forsteri*, were more abundant in the summer samples. There is little separation of the samples on the basis of station. This suggests that on most occasions, the samples at each of the four stations had a similar taxonomic composition.

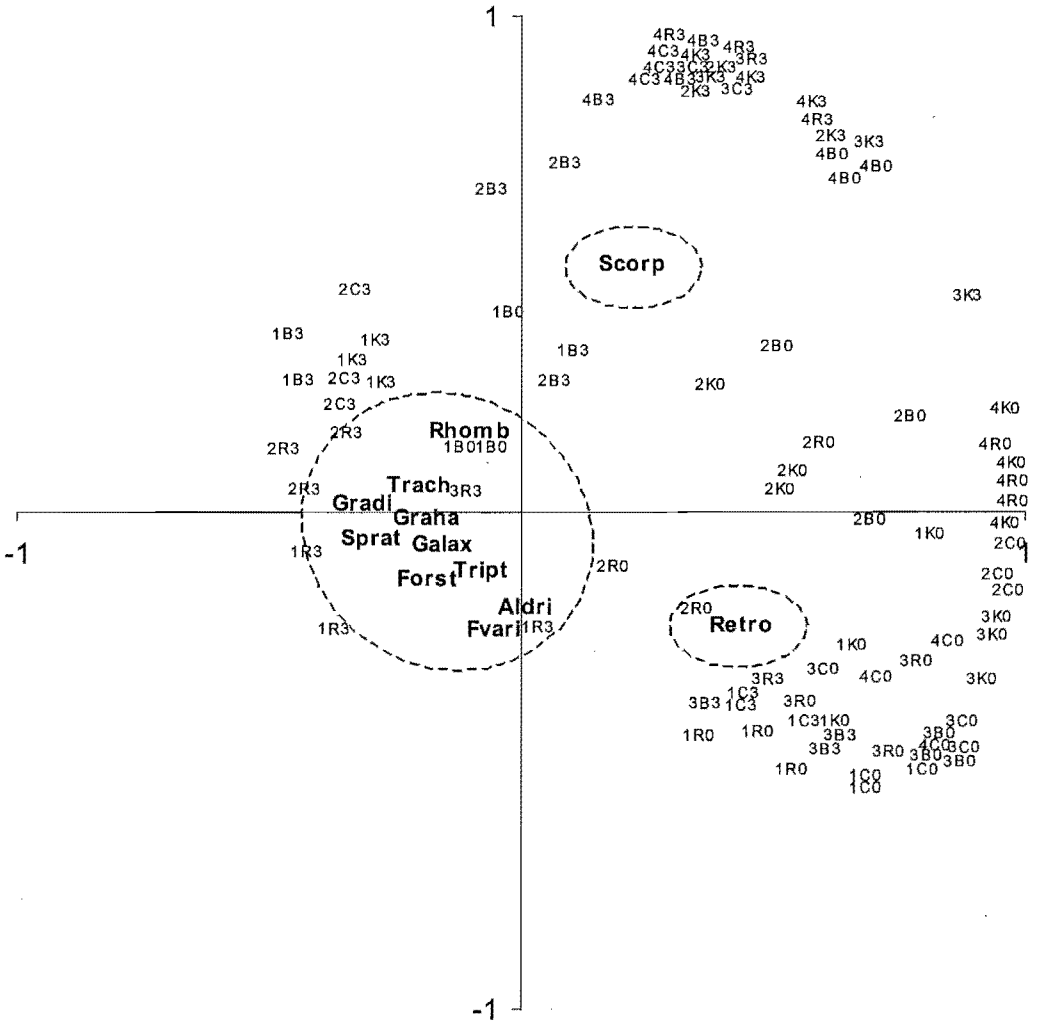

Figure 4.17. Correlation bi-plot based on Principal Components Analysis of the 96 samples taken at 2 depths (0 and 3 m), at 4 stations (Kowhai, Caves, Racecourse and Baxter's) on four occasions. Taxa codes are the first five letters of the genus or family of the 12 common taxa (except Fvari for *F. varium*). Sample codes indicate occasion/station/depth. Dotted circles indicate groupings of positively correlated taxa.

4.4 DISCUSSION

On the basis of this sampling, the hypothesis that reef fish larvae that hatch from non-pelagic eggs are retained exclusively near reefs can be rejected. Most of the common taxa, including several reef fish species, were found at all stations along the shore. Their appearance at stations away from reefs may have been due to alongshore dispersal, or larvae that have been carried offshore may have been transported back to these stations.

The four taxa that hatch from pelagic eggs or are viviparous (*Sprattus* spp., scorpaenids, *A. forsteri* and *R. plebeia*) showed no pattern in their alongshore abundance. *Sprattus* spp. and *A. forsteri* larvae were found at all stations, but the former was mainly found at 3 m and the latter at 0 m. Scorpaenid and *R. plebeia* larvae were also found at all stations, but neither showed any consistent pattern with depth. None of these taxa appeared to be retained in greater numbers near reefs. In Chapter 3, all of these taxa were found at stations up to 6 km offshore. The

alongshore (and offshore) distribution of these taxa supports the assertion that the larvae of pelagic spawners are widely dispersed (Suthers & Frank 1991).

The two freshwater demersal spawners (retropinnids and galaxiids) also showed no pattern in their alongshore abundance. Retropinnid larvae were found at all stations on most occasions and were always most abundant at 0 m. Galaxiid larvae were only found on one occasion, and then only at the Kowhai station. In Chapter 3, retropinnid larvae were found almost exclusively nearshore, but galaxiid larvae were found in large numbers at stations up to 6 km offshore. The nearshore distribution of retropinnid larvae supports the pelagic-demersal retention distinction. This taxon's larvae are carried out to the coast by rivers, but their relatively large size (McMillan 1961) implies more advanced locomotory and sensory abilities (Blaxter 1986, Miller *et al.* 1988) with which to maintain a nearshore distribution. Galaxiid larvae are also relatively large (7 - 9 mm) when they enter the marine environment (McDowall 1990), and they too should be able to maintain a nearshore distribution. However, galaxiids are a long-lived freshwater family that are likely to need their planktonic phase as a dispersal mechanism so that post-larval stages can restore populations in perturbed river systems (McDowall 1996).

Most of the reef fish taxa (all the tripterygiids except *G. capito* and *T. melobesia*) that spawn demersal eggs appeared to have no pattern in their alongshore abundance. Unidentified tripterygiid, *Forsterygion* spp. and *F. varium* larvae were found at all stations alongshore. The abundance of these taxa at the stations furthest from reefs differed between the two summer sampling occasions. In late January, the three taxa were abundant at 0 m at the stations furthest from reefs. These larvae were larger on average than those at either depth at the Baxter's station. In mid-February, there were very few larvae at 0 m at any station except Baxter's.

The larvae found at 0 m at the Kowhai, Caves and Racecourse stations in late January may have been transported alongshore directly from reef areas, or they may have arrived at these stations less directly. Tripterygiid larvae were abundant on the 27th January 1997 at the offshore stations (2 and 4 km) sampled as part of the offshore distribution study (Figures 3.8, 3.9, 3.10). It is possible that these larvae were transported shoreward by the strong onshore winds that occurred in the 36 hrs prior to sampling on the 28th January (Fig. 4.18). Prior to the mid-February sampling occasion, the winds were weaker and not onshore. If the tripterygiid larvae found at 0 m in late January are disregarded, then it appears that these taxa may have a restricted alongshore distribution. However, the offshore distribution study (Chapter 3) provides strong evidence that they do not have a restricted offshore distribution.

G. radiata larvae were found at all stations alongshore, but they were never abundant at the Baxter's station. They were only found at 3 m. Kingsford (1986) observed large abundances of *G. radiata* larvae near the substratum, particularly over sandy gutters within reefs in northeastern New Zealand. Whether *G. radiata* have a restricted offshore distribution is unknown. A single *G. radiata* larvae was caught at the 0 km station (Baxter's) in the offshore distribution study (Chapter 3). However, given the restricted depth distribution of this taxa in the alongshore study, it is unlikely that this taxa would have been present in the neuston tows further offshore.

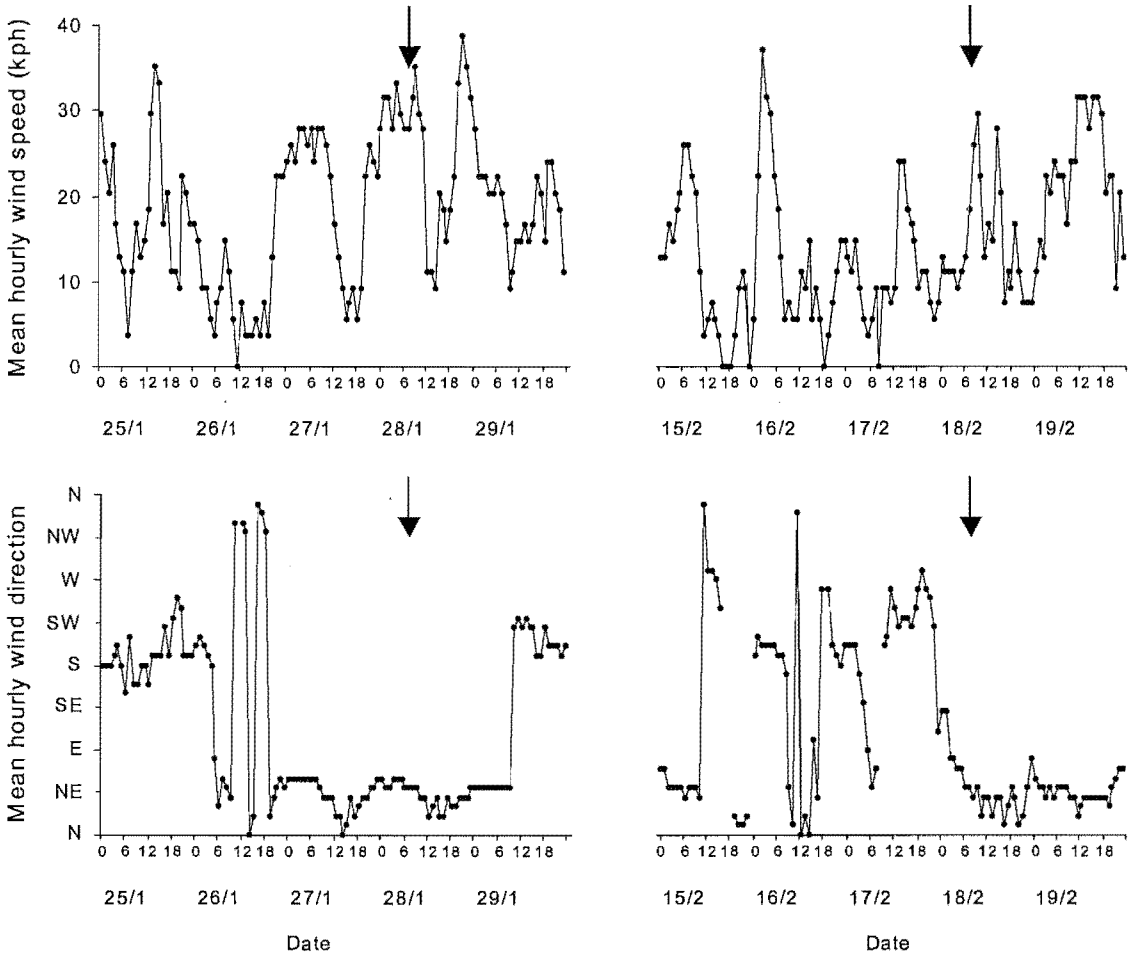

Figure 4.18. Mean hourly wind speed (kph) (upper graphs) and mean hourly wind direction (lower graphs) in the three days prior to and during each of the summer sampling occasions. The arrows indicate the start of sampling on each occasion. Data is from the Kaikoura automated weather station (G23464).

The gobiesocid, *T. melobesia*, and the tripterygiid, *G. capito*, were the only taxa which hatch from demersal eggs that had alongshore distributions indicative of retention. *T. melobesia* larvae were found at all stations, but were never abundant at the station furthest from reefs (Kowhai). They were mostly found at 3 m. Only eight of these larvae were found during the offshore distribution study (Chapter 3), but all of these were at the 0 km station (Baxter's). However, as with *G. radiata*, the restricted depth distribution of this taxon suggests it is unlikely that it would have been present in the neuston tows further offshore.

G. capito larvae were consistently more abundant at the Baxter's station than at the stations further from reefs. While this pattern suggests that *G. capito* larvae resist alongshore dispersal during their planktonic phase, there is strong evidence that their offshore distribution is not restricted. Over 6,000 *G. capito* larvae were found in neuston tows at stations between 2 and 6 km offshore during the offshore distribution study (Chapter 3). Furthermore, on most occasions there were less *G. capito* larvae at the 0 km station (Baxter's) than at the offshore stations (Table 3.4).

Several authors have found evidence of retention of tripterygiid and gobiesocid larvae near reefs throughout their development. In a study on the Canadian west coast, Marliave

(1986) collected over 20,000 gobiesocid larvae (*Gobiesox maeandricus*) in ten transects immediately above rocky reefs, but found none only 20 m offshore. Divers observed that gobiesocid larvae formed large schools and maintained their station over the more topographically complex rocky shore, resisting both offshore and alongshore displacement by currents and wave action (Marliave 1986). Marliave attributed the active inshore accumulation of these larvae to rheotactic responses, schooling behaviour and visual acuity. At dusk, when visual cues disappear and schooling breaks down, gobiesocid larvae were observed to move into closer proximity to the substrate.

In a study off northeastern New Zealand, Kingsford & Choat (1989) found greater densities of both gobiesocid and tripterygiid larvae in oblique tows near reefs as opposed to further offshore. While tripterygiid larvae were abundant in a series of neuston hauls, no gobiesocid larvae were caught near the surface. Divers also observed tripterygiid larvae close to the water surface, while gobiesocid larvae were more common at mid-depths or near the bottom. Both families were abundant in the immediate subtidal, regardless of the state of the tide, suggesting they must be capable of maintaining their position adjacent to reefs. The authors suggested that internal waves and onshore winds could facilitate the movement of tripterygiid larvae towards reefs where they have the capacity to remain. Late in the presettlement phase, a reduction in the size of the swim bladder makes tripterygiid larvae negatively buoyant, and they may settle in the shallows where they accumulate.

In a study in the Gulf of California, Brogan (1994a) found that there was no difference between the abundance of tripterygiid and gobiesocid larvae at stations 1 and 20 m offshore from reefs, but by 100 m densities had dropped between 90 - 97%. Between samples taken with light traps and those taken using a plankton net, all pelagic size classes of these families were found over reefs. Neither family was present in samples taken beyond 5 km from shore in an earlier study (Moser *et al.* 1973). While these concentration gradients are consistent with larval retention, Brogan indicates that larvae could have been transported away from reefs in the longshore direction to sandy shores where he did not sample.

The results of my study and the findings of Chapter 3 contrast markedly with the three studies described above. The gobiesocid larvae and most of the tripterygiid larvae appeared to resist major alongshore dispersal in this study. However, there was no evidence that tripterygiid larvae were more abundant inshore. This poses the question: how can a taxon have a restricted distribution alongshore but not offshore?

It is likely that fish in the immediate subtidal can see a reef and respond to its presence (Kingsford & Choat 1989). In the absence of favourable currents and eddies to retain larvae near reefs, larvae may maintain their position through active swimming (Leis 1982). Larvae may also prefer the more turbulent flow regime along complex rocky shores, and avoid more laminar velocity gradients along sandy shores (Marliave 1986). Presettlement schooling may also assist in the retention of both gobiesocid and tripterygiid larvae over reefs.

Presettlement schooling is a common behaviour of temperate benthic fishes. Marliave (1986) observed that presettlement larvae from five families of eastern Pacific intertidal and reef fish (Gobiesocidae, Cottidae, Stichaeidae, Pholidae and Gasterosteidae) schooled in close

proximity to the substratum. Presettlement schooling has also been observed for hexagrammid and clinid larvae near the substrate in southern Californian kelp beds (M. H. Carr unpublished data, cited in Breitburg 1989) and for tripterygiid larvae on Tasmanian reefs (R. E. Thresher unpublished data, cited in Breitburg 1989). Near-bottom schooling behaviour was also observed for gobiid larvae in Chesapeake bay (Breitburg 1989). Kingsford (1986) observed aggregations of both tripterygiid larvae and gobiesocid larvae near reefs in northeastern New Zealand.

If the mechanisms described above are effective at preventing alongshore dispersal, they, together with onshore winds, should also prevent offshore dispersal. However, particularly in the case of tripterygiid larvae, this does not seem to be the case along the Kaikoura coast. It has been shown that tidal currents alone, even along a straight coast, can produce complex distribution patterns (Richards *et al.* 1995). Can local hydrodynamics explain the distribution of some demersal spawning reef fish larvae at Kaikoura?

The predominant wind-derived water transport at Kaikoura is towards the north-west, and thus onshore during all seasons (Heath 1972b). This onshore movement of surface water should retain the majority of ichthyoplankton in the nearshore environment. However, the onshore motion of surface waters is likely to produce coastal downwelling, which may produce offshore bottom layer transport that could transport larvae offshore. In the summer months, this water motion, together with known upwelling at the shelf break (Garner 1961), could produce a cross-shelf recirculation cell similar to that described by Smith *et al.* (1999) for the Sydney shelf. This recirculation cell, although acting to disperse tripterygiid larvae across the shelf, would also ensure that larvae were retained within shelf waters and be transported shoreward if in surface waters. The existence of such a circulation cell can only be determined with further studies of both ichthyoplankton distributions and hydrodynamics in the nearshore and shelf regions along the Kaikoura coast.

Larvae returning to the nearshore environment as a result of cross-shelf advection may still not encounter a suitable habitat for settlement. The large tripterygiid larvae found in the surface layer at the stations away from reefs are dependent on alongshore currents to transport them to reef areas. For larvae which are competent to settle, this delay will prolong their larval phase and expose them to further mortality.

With an increased knowledge of, and thus an increased ability to identify, the larval stages of many species of temperate reef fish, there is little benefit in grouping families together and describing their distribution in relation to reefs. Several authors have reported inconsistencies within families in the distribution patterns attributed to the family as a whole. Marliave (1986) reported that the genus *Artedius*, within the family Cottidae, had an offshore distribution distinct from other members of the same family. Kingsford & Choat (1989) and Tricklebank (1992) reported inconsistencies in the Tripterygiidae, with larvae from the genus *Forsterygion* frequently being found offshore. Brogan (1994a) identified two possible groupings of Gobiidae: those species that were concentrated over reefs and those that were more abundant offshore. However, each of these families has been described as having "inshore" larvae. Clearly, there are species-specific patterns of offshore and alongshore distribution which are masked by grouping families together.

In the Kaikoura region, many taxa belonging to the tripterygiid family, although possibly able to resist alongshore dispersal, do not have an inshore distribution. The offshore dispersal of their larvae will expose them to unfavourable advection and as a result their recruitment is likely to be inconsistent (Suthers & Frank 1991).

Chapter Five

Fine-Scale Patterns of Vertical Distribution in Larval Fish

5.1 INTRODUCTION

When investigating the distribution of fish larvae, it is important to realise that ichthyoplankton exist in three dimensions in the pelagic environment. Studies that concentrate on the horizontal distribution of ichthyoplankton are essential for understanding large scale movement patterns. However, the vertical distribution of fish larvae must not be neglected. Gradients in light level, temperature, hydrostatic pressure and food availability are much greater in the vertical plane than in the horizontal plane (Laprise & Dodson 1993). Thus, the vertical distribution of fish larvae is likely to be more defined, because abundances will change rapidly with depth.

Given a specific relationship between depth and many of the environmental variables (e.g., light, temperature, hydrostatic pressure and food) that are important to larval fish survival, it might be expected that the larvae of individual fish species would occupy a very narrow and relatively constant depth band defined by simple causal relationships with these variables. However, this is not usually the case for two reasons. First, the combined effects of both large and small scale hydrographic events (e.g., tides, currents, upwelling and wave action) act to mix any possible layers near the surface and thereby disrupt the vertical distribution of larval fish. Second, many taxa of both marine and freshwater ichthyoplankton undergo diel vertical migrations with amplitudes from a few to hundreds of metres (Smith *et al.* 1978, Kendall & Naplin 1981, Boehlert *et al.* 1985, Yamashita *et al.* 1985, Sogard *et al.* 1987, Davis *et al.* 1990).

Diel vertical migration of marine larval fish is well documented (see review by Neilson & Perry 1990). These migrations range between 'nocturnal ascent' (Smith *et al.* 1978, Perry & Neilson 1988) where larvae move up in the water column at the onset of night and down with the onset of day, and 'nocturnal descent' (Yamashita *et al.* 1985, Lyczkowski-Schultz & Steen 1991) where larvae move down with the onset of night and up with the onset of day. Fish larvae may also display a distinct depth preference during the day with random distribution at night or 'nocturnal diffusion' (Leis 1991b, Haldorson *et al.* 1993, Jenkins *et al.* 1998).

The adaptive value of vertical migration is still in dispute, but hypothesised reasons include predator avoidance (Brewer *et al.* 1984, Lampert 1989, Brodeur & Rugen 1994), prey tracking (Fortier & Leggett 1984, Brewer & Kleppel 1986, Munk *et al.* 1989), thermoregulation (Neverman & Wurtsbaugh 1994), energy conservation (Hunter & Sanchez 1976, Heath 1992), dispersal (Smith *et al.* 1978, Fortier & Leggett 1982, Norcross & Shaw 1984, Cowen *et al.* 1993) or acting as a retention mechanism (Marliave 1986). The situation is further complicated by the fact that the magnitude and amplitude of vertical migration often changes during ontogenetic development (Brewer & Kleppel 1986, Perry & Neilson 1988).

The degree to which diel vertical migration of fish larvae is controlled by endogenous rhythmicity is controversial (Neilson & Perry 1990). Light intensity, food supply, temperature, tides and predator avoidance are important in mediating diel vertical migrations (see review by Neilson & Perry 1990). However, vertical migration in marine fishes appears to be a labile process that can be significantly influenced by local conditions and which can often be site/time specific (Barnett *et al.* 1984, Leis 1991b, Heath 1992, Lough & Potter 1993). These local variations may mask any detectable and consistent expression of endogenous rhythmicity.

Knowledge of the vertical distributions of fish larvae and how they vary over differing temporal and spatial scales is crucial to understanding the ecological mechanisms and processes that influence their dispersal and transport and to the assessment of abundance. Sampling at a single depth may substantially underestimate the abundance of a species with a narrow depth distribution. Therefore, it is important that both the vertical and horizontal distributions of ichthyoplankton be studied, because together they provide far greater insight into the factors influencing the distribution, movement and subsequent recruitment of fish larvae.

This chapter investigates the fine-scale patterns of vertical distribution of larval fishes at an inshore site on the Kaikoura Peninsula. In Chapter 4, I found that the larvae of many taxa have stratified vertical distributions in surface waters around the Peninsula. However, it is not known whether the observed fine-scale patterns of vertical distribution are maintained at night. The purpose of this study was to investigate whether the vertical distribution of larval fish in surface waters at a nearshore site was consistent through time.

Light intensity is known to be important in regulating the vertical distribution of larval fish (Johansen 1925, Blaxter 1975, Neilson & Perry 1990), so the phase of the moon was incorporated into this study. Season was also incorporated as a factor. The null hypotheses tested were:

1. The abundance of larval fish does not change with depth.
2. The vertical distribution of larval fish does not change with the time of day.
3. The vertical distribution of larval fish does not change with the phase of the moon.
4. The vertical distribution of larval fish does not change with season.

Most studies of the vertical distribution of ichthyoplankton have concentrated on depth scales ranging from tens (Pritchett & Haldorson 1989, Lyczkowski-Schultz & Steen 1991, Haldorson *et al.* 1993) to hundreds (Ahlstrom 1959, Boehlert & Mundy 1994, Brodeur & Rugen 1994) of metres. As a study of this scale was not logistically possible in this investigation, sampling was concentrated in the waters very close to the surface (< 3 m depth). Most studies of the vertical distribution of fish larvae incorporate these depths into a single "surface" sample and any fine-scale variation in the vertical distribution of neustonic larval fish is obscured. The surface waters around the Kaikoura Peninsula have been found to contain an abundant and diverse assemblage of larval fish. By focussing this study of fine-scale distribution patterns on the uppermost 3 m of the water column, any fine-scale variation in vertical distribution by neustonic or "facultative neustonic" (Hempel & Weikert 1972) larvae should be detected.

5.2 METHODS

5.2.1 Sampling procedure

Repeated sampling was done at a single key site on the southern side of the Kaikoura Peninsula (Fig. 5.1). Diverse larval fish assemblages had been found in the surface waters at this site during studies of offshore and alongshore distribution. The site was 50 m offshore from a rocky shoreline within South Bay. It had an average depth of 12 m of water and the bottom was composed of sand and small (< 5 m^2) rocky patch reefs. The site was sampled during 8 periods (Table 5.1). These periods encompassed two seasons and full and new moons (x2)

within each season. On the first day of each period the site was sampled in the afternoon (c. 1400 hrs) and again at night (2 hrs after sunset). The site was sampled a third time the following morning (2 hrs after sunrise). Night sampling was restricted to cloudless nights to standardise ambient light levels.

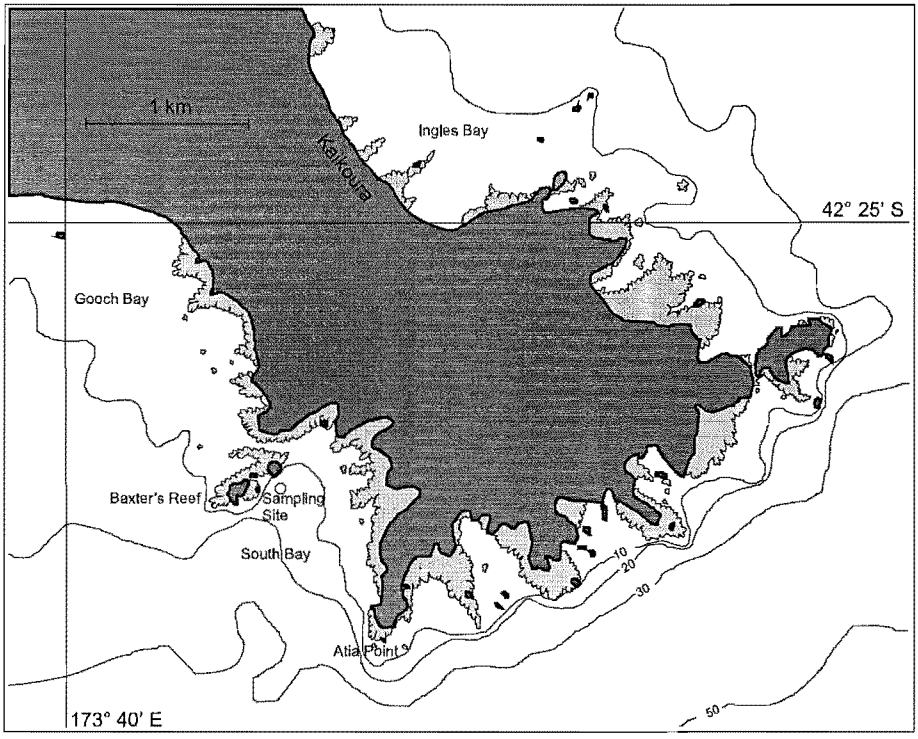

Figure 5.1. Map of the Kaikoura Peninsula on the northeast coast of the South Island. The sampling site within South Bay is shown. Bathymetry is in metres.

Table 5.1. Sampling dates with season, moon phase and date of the associated phase peak.

Sampling Dates	Season	Phase	Phase Peak
4th - 5th March 1996	Autumn	Full	5th March
7th - 8th March 1996			
14th - 15th March 1996	Autumn	New	19th March
17th - 18th March 1996			
10th - 11th December 1996	Summer	New	11th December
12th - 13th December 1996			
21st - 22nd January 1997	Summer	Full	24th January
24th - 25th January 1997			

On each occasion, three replicate 15 minute tows were done at each of three depths (surface (0 m), 1 m and 3 m). The various depths were sampled in random order and the three replicate tows within each depth were made consecutively over a total period of no longer than one hour. Each sampling episode (3 depths x 3 replicates) lasted no more than three hours.

Ichthyoplankton was sampled using a plankton net with a 707 x 707 mm mouth (0.5 m^2) and 280 µm mesh. The net was a box-pyramid design with a filtration efficiency of 1:11. A

General Oceanics flowmeter (Model 2030R) was fitted in the mouth of the net (at 0.33 of the net width) to determine the volume of water filtered per tow. The net was rigged to be towed alongside a 6 m boat to avoid disturbance caused by the wake. The top of the net frame was suspended from a gantry so that it sampled with the uppermost edge of the net at a fixed depth. A 25 kg Scripps depressor was suspended from the lower edge of the frame to keep the net mouth vertical in the water column. The net was towed with a four-point bridle that joined above the net mouth to avoid disturbance caused by the wire strops.

During surface samples (0 m), the upper edge of the mouth of the net was held at approximately 10 cm above the surface of the water (Fig. 2.8). The flowmeter was submerged at all times. For 1 m and 3 m samples, the upper edge of the mouth of the net was held at 1 m and 3 m below the surface of the water, respectively. The net was towed at c. 1.2 m s^{-1} and the average volume filtered was 450 m^3. At the completion of each tow, the boat was stopped before the net was raised to avoid contamination of the sample with fish larvae from higher in the water column. The net was washed thoroughly with pumped seawater after each tow and the samples were immediately preserved in buffered 10% formalin in seawater.

All fish larvae were removed from the samples using a dissection rnicroscope, identified to the lowest possible taxonomic level, counted and stored in buffered 2% formalin in freshwater. Counts were standardised to the number of fish per 500 m^3. Clupeid, retropinnid and galaxiid larvae could not be identified beyond the family or genus level because of the similarities of larvae from individual species and the presence of adults from several species of each of these families in the study area. Small scorpaenids, labrids, tripterygiids, centrolophids and pleuronectids could also not be identified below the family or genus level.

The volume of the zooplankton in each sample, after fish larvae had been removed, was measured by displacement and converted to ml per 500 m^3. Any drift algae or flotsam were removed before volumes were measured.

5.2.2 Analysis

The ichthyoplankton samples contained a wide range of taxa, allowing tests on the temporal and spatial distribution of individual taxa and on species richness. Five-factor ANOVAs, with season (summer and autumn), moon phase (full and new), time (afternoon, night and morning), depth (0 m, 1 m and 3 m) and occasion (x 2) (treated as random) as factors, were used to compare the abundance of commonly occurring taxa (> 0.5% of the total number caught), all taxa and species richness. Prior to ANOVA, the data for each taxon were tested for homogeneity of variances using Cochran's test and all data became homogeneous when log (x+1) transformed. Initial ANOVA revealed no significant difference ($p > 0.25$) between the two occasions within each combination of factors, so the data were pooled and retested omitting occasion as a factor.

Correlation analysis was used to investigate any similarities in the occurrence of common taxa. The abundance of each taxon in the three replicates on each of the two occasions was pooled, log(x+1) transformed and correlated with other common taxa. The

resulting correlation matrix was corrected for multiple comparisons using an adjusted α level (Ezekiel 1945) derived from the equation

$$\alpha_{corrected} = \frac{0.05}{no.\ of\ correlations}$$

Principal Components Analysis (PCA) was used to display the relationship between the taxonomic composition of the samples. Data were log(x+1) transformed prior to PCA.

5.3 RESULTS

In total, the 216 samples collected 51,130 larvae from 31 families (Table 5.2). Sixty-eight taxa were identified, including eight that contained more than one species and fifteen unidentified taxa. The damaged category contains larvae that were unidentifiable as a result of damage during capture. The two most abundant taxa, Unidentified Scorpaenidae (36.4%) and Unidentified Tripterygiidae (32.9%), accounted for 69% of the total catch. Fifty-three taxa each comprised < 0.5% of the total number of larvae collected. Of the fifteen more common taxa, only *Forsterygion varium* and *Arnoglossus scapha* occurred in less than 30% of the samples. Instead of occurring in very low numbers throughout many samples, most of the less numerous taxa occurred in only a few samples (Table 5.2). Eighteen taxa occurred in only a single tow (0.5% occurrence).

Abundances of the fifteen common taxa were consistent between each of the sampling occasions within a season and moon phase. ANOVA showed no significant difference ($p > 0.25$) between the abundance of each of the fifteen common taxa on the two occasions, so data were combined and "occasion" was removed as a factor in further analyses.

Table 5.2. Composition of samples. Total abundance (n), percentage of total catch when adjusted for volume (%) and percentage occurrence in the 216 samples (% Occ) is given for each taxon.

Family	Taxon	n	%	% Occ
Clupeidae	*Sprattus* spp.	941	1.9	42.6
Retropinnidae	Unidentified Retropinnidae	1712	2.6	31.5
Galaxiidae	*Galaxias maculatus*	1	< 0.1	0.5
Sternoptychidae	*Maurolicus muelleri*	1	< 0.1	0.5
Myctophidae	*Diaphus* spp.	1	< 0.1	0.5
	Gymnoscopelus piabilis	1	< 0.1	0.5
	Lampanyctodes hectoris	3	< 0.1	0.9
	Symbolophorus boops	35	< 0.1	4.6
Moridae	Unidentified Moridae	4	< 0.1	1.4
	Auchenoceros punctatus	20	< 0.1	4.6
	Pseudophycis bachus	3	< 0.1	1.4
Gobiesocidae	*Diplocrepis puniceus*	533	1.0	37.5
	Trachelochismus melobesia	3172	6.4	59.7
	Trachelochismus pinnulatus	52	0.1	13.4
Hemiramphidae	*Hyporhamphus ihi*	7	< 0.1	2.8
Trachichthyidae	*Paratrachichthys trailli*	7	< 0.1	3.2
Syngnathidae	*Hippocampus abdominalis*	104	0.2	17.1
	Leptonotus elevatus	7	< 0.1	3.2
	Lissocampus filum	92	0.2	29.2
	Leptonotus norae	2	< 0.1	0.9
Scorpaenidae	Unidentified Scorpaenidae	19196	36.4	82.4
Triglidae	*Chelidonichthys kumu*	108	0.2	18.1
Acanthoclinidae	*Acanthoclinus fuscus*	466	0.9	30.1
Carangidae	*Trachurus declivis*	1	< 0.1	0.5
Latrididae	*Mendosoma lineatum*	37	0.1	8.8
Mugilidae	*Aldrichetta forsteri*	61	0.1	13.0
Labridae	*Notolabrus celidotus*	7	< 0.1	2.3
Odacidae	*Odax pullus*	1	< 0.1	0.5
Uranoscopidae	*Genyagnus monopterygius*	6	< 0.1	2.3
Creediidae	Unidentified Creediidae	161	0.2	4.2
	Limnichthys rendahli	23	< 0.1	6.5
Leptoscopidae	*Crapatalus novaezealandiae*	5	< 0.1	1.9
Percophidae	*Hemerocoetes monopterygius*	23	< 0.1	3.7
Tripterygiidae	Unidentified Tripterygiidae	16103	32.9	80.1
	Bellapiscis medius	2	< 0.1	0.5
	Forsterygion lapillum	799	1.6	40.7
	Forsterygion varium	363	0.7	26.4
	Gilloblennius tripennis	282	0.5	40.3
	Grahamina capito	2911	5.5	63.4
	Notoclinus fenestratus	13	< 0.1	3.7
	Ruanoho decemdigitatus	1372	3.1	52.8
Clinidae	*Cologrammus flavescens*	70	0.1	9.3
	Cristiceps aurantiacus	31	< 0.1	7.4
Eleotrididae	*Grahamichthys radiata*	1006	2.1	35.2
Gobiidae	*Gobiopsis atrata*	216	0.4	29.6
Gempylidae	*Thyrsites atun*	35	0.1	7.9
Centrolophidae	*Seriolella brama*	98	0.2	12.5
Bothidae	*Arnoglossus scapha*	420	0.8	20.4
	Lophonectes gallus	6	< 0.1	2.3
Pleuronectidae	*Peltorhamphus* spp.	248	0.4	20.4
	Rhombosolea plebeia	267	0.5	38.9
	Rhombosolea retiaria	3	< 0.1	1.4
Monacanthidae	*Parika scaber*	5	< 0.1	2.3
Unknown	Damaged	8	< 0.1	1.9
	Unidentified Species 1	46	0.1	8.8
	Unidentified Species 2	1	< 0.1	0.5
	Unidentified Species 3	1	< 0.1	0.5
	Unidentified Species 4	15	< 0.1	2.8
	Unidentified Species 7	1	< 0.1	0.5
	Unidentified Species 8	3	< 0.1	1.4
	Unidentified Species 9	1	< 0.1	0.5
	Unidentified Species 10	2	< 0.1	0.5
	Unidentified Species 11	1	< 0.1	0.5
	Unidentified Species 12	1	< 0.1	0.5
	Unidentified Species 13	2	< 0.1	0.9
	Unidentified Species 14	1	< 0.1	0.5
	Unidentified Species 15	2	< 0.1	0.5
	Unidentified Species 18	1	< 0.1	0.5
	Unidentified Species 19	1	< 0.1	0.5
Total		51130		

Table 5.3. Summary results from ANOVA of the abundance of all taxa combined, taxonomic richness and fifteen common taxa with season (summer and autumn), moon phase (full and new), time (afternoon, night and morning) and depth (0 m, 1 m and 3 m) as factors. The variance has been partitioned (%) for each factor and for the interaction terms. Significance is indicated (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$).

		Season	Moon	Time	Depth	S x M	S x T	M x T	S x D	M x D	T x D	S x M x T	S x M x D	S x T x D	M x T x D	S x M x T x D	Residual
	df	1	1	2	2	1	2	2	2	2	4	2	2	4	4	4	180
All taxa	F	40.0***	178.1***	257.3***	360.5***	314.7***	3.0	19.8***	22.1***	103.2***	3.0*	72.5***	15.8***	9.0***	10.6***	19.9***	
	%	1.5	6.9	19.9	27.8	12.1	0.2	1.5	1.7	8.0	0.5	5.6	1.2	1.4	1.6	3.1	6.9
Taxonomic	F	2.5	90.1***	454.7***	98.1***	125.7***	2.3	11.6***	12.8***	14.0***	9.9***	7.4**	18.7***	3.5**	17.1***	16.4***	
Richness	%	0.1	4.9	49.8	10.7	6.9	0.3	1.3	1.4	1.5	2.2	0.8	2.0	0.8	3.7	3.6	9.9
Sprattus spp.	F	129.6***	57.0***	164.8***	49.9***	23.4***	18.2***	25.6***	30.5***	17.9***	13.4***	19.1***	3.3*	7.2***	15.2***	14.4***	
	%	10.4	4.6	26.4	8.0	1.9	2.9	4.1	4.9	2.9	4.3	3.1	0.5	2.3	4.9	4.6	14.4
Retropinnidae	F	621.2***	3.0	41.4***	166.4***	0.8	52.7***	6.1**	175.9***	5.9**	72.4***	6.3**	4.6*	65.2***	10.0***	7.8***	
	%	26.5	0.1	3.5	14.2	0.0	4.5	0.5	15.0	0.5	12.3	0.5	0.4	11.1	1.7	1.3	7.7
D. puniceus	F	15.6***	59.4***	186.1***	65.6***	47.2***	17.5***	19.5***	6.4**	38.9***	19.8***	17.1***	16.9***	20.9***	11.0***	12.2***	
	%	1.2	4.6	28.8	10.1	3.6	2.7	3.0	1.0	6.0	6.1	2.6	2.6	6.5	3.4	3.8	13.9
T. melobesia	F	0.9	39.0***	95.9***	172.0***	58.5***	70.9***	16.0***	22.3***	36.2***	8.3***	21.6***	11.0***	5.6***	10.4***	9.2***	
	%	0.1	3.0	14.7	26.4	4.5	10.9	2.5	3.4	5.6	2.6	3.3	1.7	1.7	3.2	2.8	13.8
Scorpaenidae	F	29.1***	987.2***	78.1***	15.9***	182.8***	3.0	71.4***	39.2***	14.7***	19.2***	13.4***	38.1***	16.4***	9.6***	9.7***	
	%	1.4	46.0	7.3	1.5	8.5	0.3	6.7	3.7	1.4	3.6	1.2	3.5	3.1	1.8	1.8	8.4
A. fuscus	F	231.1***	27.7***	236.3***	10.7***	47.6***	109.7***	10.7***	16.8***	3.9*	3.2*	23.6***	10.9***	5.0**	1.1	4.6**	
	%	16.7	2.0	34.1	1.5	3.4	15.8	1.5	2.4	0.6	0.9	3.4	1.6	1.4	0.3	1.3	13.0
Tripterygiidae	F	196.7***	36.8***	221.9***	353.3***	243.7***	1.6	11.6***	30.7***	30.8***	1.0	29.9***	18.7***	3.3*	11.9***	11.0***	
	%	9.1	1.7	20.5	32.7	11.3	0.1	1.1	2.8	2.9	0.2	2.8	1.7	0.6	2.2	2.0	8.3
F. lapillum	F	0.1	16.5***	135.7***	40.6***	36.8***	0.2	48.8***	10.0***	0.2	25.6***	21.7***	12.8***	1.3	4.3**	11.4***	
	%	0.0	1.7	28.8	8.6	3.9	0.0	10.3	2.1	0.0	10.8	4.6	2.7	0.5	1.8	4.8	19.1
F. varium	F	1.0	47.6***	55.5***	35.0***	12.2**	0.5	56.4***	10.8***	12.2***	22.4***	9.2***	2.3	2.5*	8.5***	7.2***	
	%	0.1	6.2	14.5	9.1	1.6	0.1	14.7	2.8	3.2	11.7	2.4	0.6	1.3	4.5	3.7	23.5
G. tripennis	F	37.0***	7.8**	54.7***	19.7***	23.4***	1.6	1.9	8.8***	6.0**	9.2***	37.7***	16.7***	2.7*	1.7	9.2***	
	%	5.8	1.2	17.3	6.2	3.7	0.5	0.6	2.8	1.9	5.8	11.9	5.3	1.7	1.1	5.8	28.4
G. capito	F	646.8***	1.6	15.4***	116.3***	0.0	22.3***	14.5***	24.0***	31.0***	24.9***	14.4***	31.6***	2.9*	27.1***	23.4***	
	%	38.5	0.1	1.8	13.8	0.0	2.6	1.7	2.9	3.7	5.9	1.7	3.8	0.7	6.5	5.6	10.7
R. decemdigitatus	F	220.5***	23.5***	182.3***	13.1***	14.2***	33.4***	29.5***	2.8	18.6***	2.7*	0.7	29.8***	0.6	5.2**	0.8	
	%	20.1	2.1	33.3	2.4	1.3	6.1	5.4	0.5	3.4	1.0	0.1	5.4	0.2	1.9	0.3	16.4
G. radiata	F	79.4***	110.6***	344.9***	98.4***	79.3***	23.1***	34.7***	5.7**	19.7***	28.1***	33.5***	3.6*	9.4***	14.1***	33.2***	
	%	4.1	5.8	36.0	10.3	4.1	2.4	3.6	0.6	2.1	5.9	3.5	0.4	2.0	3.0	6.9	9.4
A. scapha	F	732.8***	780.8***	194.5***	65.3***	652.3***	174.3***	174.7***	43.9***	59.8***	25.0***	157.3***	38.3***	12.8***	31.3***	15.9***	
	%	16.3	17.3	8.6	2.9	14.5	7.7	7.8	1.9	2.7	2.2	7.0	1.7	1.1	2.8	1.4	4.0
R. plebeia	F	29.0***	99.9***	133.7***	12.1***	3.6	23.1***	15.5***	9.9***	23.1***	2.6*	2.4	1.6	4.0**	3.7**	2.1	
	%	3.6	12.4	33.2	3.0	0.4	5.7	3.8	2.5	5.7	1.3	0.6	0.4	2.0	1.8	1.1	22.4
Plankton volume	F	26.7***	3.0	391.5***	9.6***	85.6***	11.8***	16.8***	12.8***	27.3***	19.6***	72.8***	15.9***	15.1***	22.8***	34.6***	
	%	1.6	0.2	46.8	1.2	5.1	1.4	2.0	1.5	3.3	4.7	8.7	1.9	3.6	5.5	8.3	4.3

Of the single factors, depth and time had the greatest effects, being significant in all cases and usually accounting for a relatively large percentage of the total variation (Table 5.3). Overall, three times more larvae were found at 1 m than at 0 m, and five times more larvae were found at 3 m than at 0 m (Fig. 5.2). More larvae were found at all three depths at night, but this pattern varied between seasons and phases of the moon. Fewer larvae were found at 0 m during a new moon than during a full moon in summer and autumn.

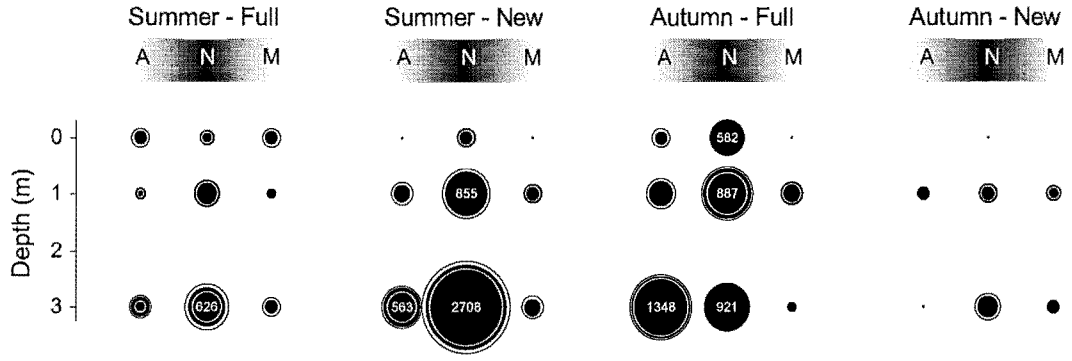

Figure 5.2. The mean abundance ± SE (per 500 m^3) of larvae from all taxa found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

The total catch of larval fish ranged from a single sample taken at 3 m depth at night during a new moon in summer that caught 3204 larval fish from twelve different taxa, to a sample taken at 0 m in the afternoon during a new moon in autumn that caught only one larval fish.

Time had the single greatest effect on the taxonomic richness of the samples (Table 5.3). Overall, twice as many taxa were found at night as during the day (Fig. 5.3). Fewer taxa were found at 0 m than at the other two depths during the day, but at night the depth distribution became more uniform.

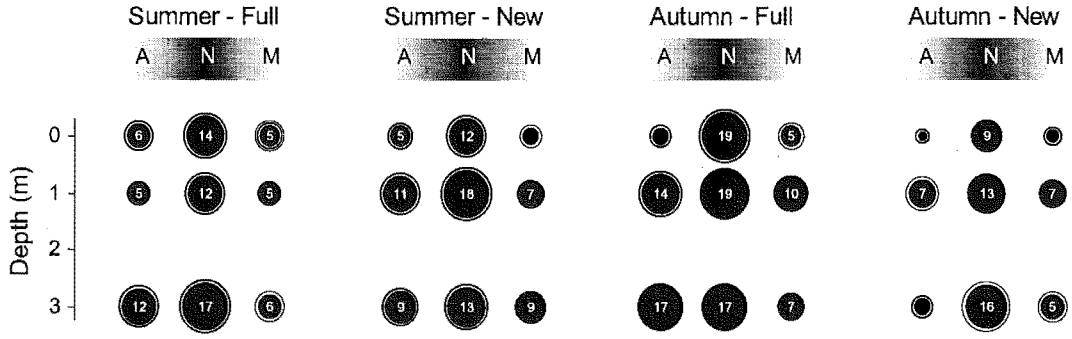

Figure 5.3. The mean taxonomic richness ± SE (per 500 m^3) found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

The taxonomic richness of the samples ranged from one, for several samples taken in the afternoon during a new moon in autumn, to twenty, for two samples taken at night during a full moon in autumn. The overall mean taxonomic richness was 9.5 taxa per sample.

Time had the single greatest effect on the abundance of *Sprattus* spp. larvae (Table 5.3). *Sprattus* spp. larvae were twenty times more abundant during the afternoon and night than during the morning (Fig. 5.4). Overall, ten times more larvae were found during autumn than during summer. On average, more larvae were found at 3 m than at the other two depths, but this pattern was dependent on the season, moon phase and time.

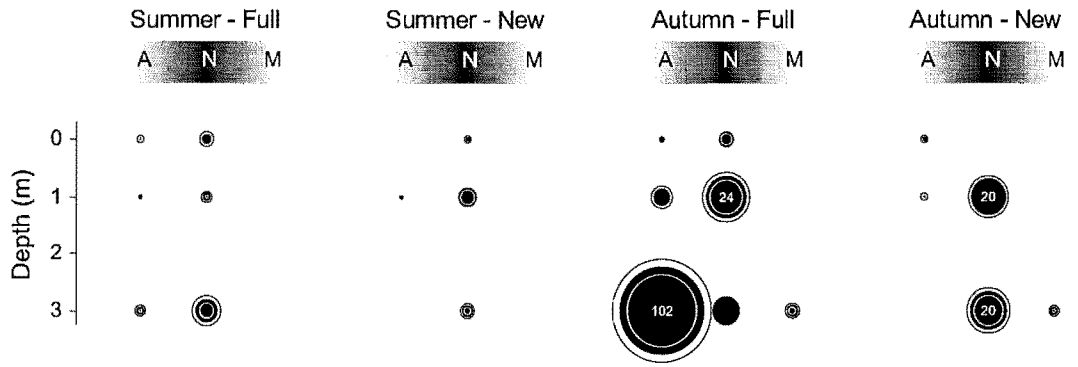

Figure 5.4. The mean abundance ± SE (per 500 m^3) of *Sprattus* spp. larvae found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

Sprattus spp. larvae appear to undergo nocturnal ascent, with more larvae being found in the uppermost 3 m of water at night than during the day. Very few larvae of this species were found during the morning tows.

Season had the single greatest effect on the abundance of retropinnid larvae (Table 5.3). Only three larvae were found during summer and these were all found at night. Retropinnid larvae were twenty times more abundant during the afternoon and morning than during the night (Fig. 5.5). Most retropinnid larvae were found at 1 m depth in the afternoon and morning during autumn. There was little difference between phases of the moon in the average number of retropinnid larvae found.

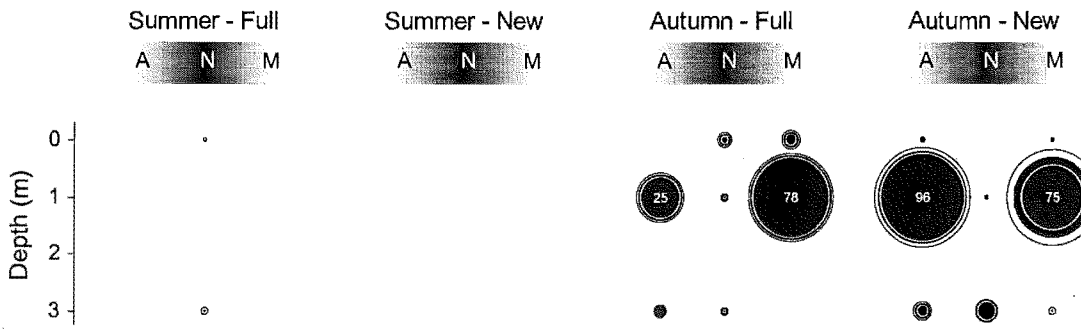

Figure 5.5. The mean abundance ± SE (per 500m^3) of retropinnid larvae found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

Retropinnid larvae appear to undergo nocturnal descent, with more larvae being found in the uppermost 3 m of water during the day than at night. The large number of larvae that were present at 1 m during the day were absent at night.

Time had the single greatest effect on the abundance of *Diplocrepis puniceus* larvae (Table 5.3). Overall, eight times more *D. puniceus* larvae were found at night than during the day (Fig. 5.6), but this pattern was more obvious in summer than in autumn. On average, fewer larvae were found at 0 m than at 1 or 3 m, but this pattern was dependent on time and season.

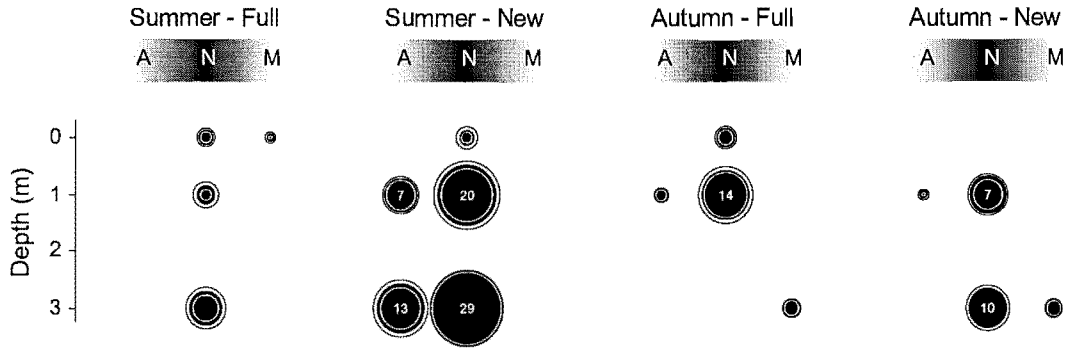

Figure 5.6. The mean abundance ± SE (per 500m^3) of *Diplocrepis puniceus* larvae found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

D. puniceus larvae appear to undergo nocturnal ascent, with more larvae being found in the uppermost 3 m of water at night than during the day. During the afternoon, most larvae were found at 1 and 3 m, but at night, larvae were also found at 0 m. Few larvae were found during the morning tows, and the majority of these were found at 3 m.

Depth had the single greatest effect on the abundance of *Trachelochismus melobesia* larvae (Table 5.3). Overall, five times more larvae were found at 3 m than at the other two depths (Fig. 5.7), but this pattern was more evident in summer than autumn. More *T. melobesia* larvae were found at night at all depths during summer, but not in autumn.

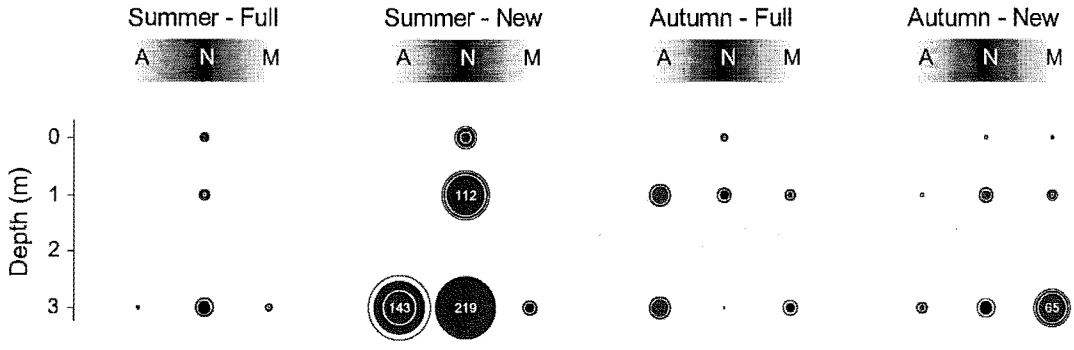

Figure 5.7. The mean abundance ± SE (per 500m^3) of *Trachelochismus melobesia* larvae found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

If *T. melobesia* larvae have a diel vertical migration pattern, then it is unclear at this fine spatial scale. At 0 m, larvae numbers increased at night during both seasons and phases of the moon. The same is true at 1 m in summer, but not in autumn. At 3 m, larval abundance is very variable, with large numbers of larvae being found during the day and night.

Moon phase had the single greatest effect on the abundance of scorpaenid larvae (Table 5.3). Overall, twenty times more larvae were found during a full moon than during a new moon (Fig. 5.8), but this pattern was less evident in summer than in autumn. Larvae were more abundant at night than during the morning, but larval abundance did not appear to change significantly between afternoon and night.

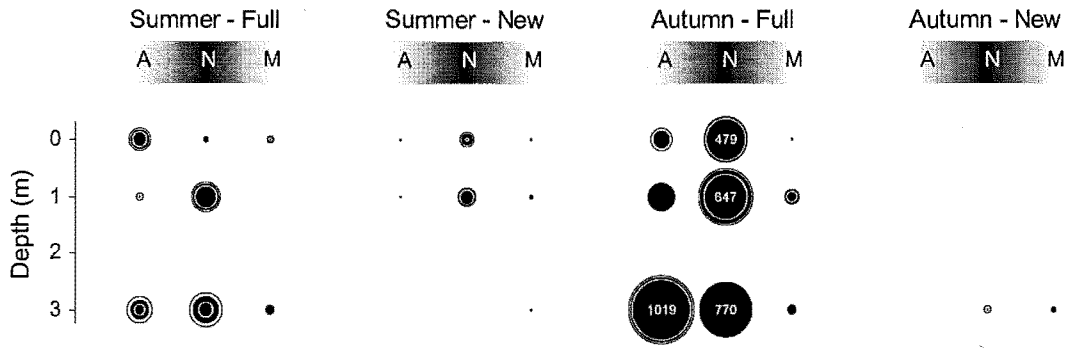

Figure 5.8. The mean abundance ± SE (per 500m^3) of scorpaenid larvae found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

Scorpaenid larvae appear to undergo nocturnal ascent, with more larvae being found in the uppermost 3 m of water in the afternoon and evening than during the morning.

Time had the single greatest effect on the abundance of *Acanthoclinus fuscus* larvae (Table 5.3). Overall, twenty-five times more larvae were found at night than during the afternoon or morning (Fig. 5.9). Larvae were considerably more abundant in summer than autumn, and there were three times more larvae found during a new moon than a full moon.

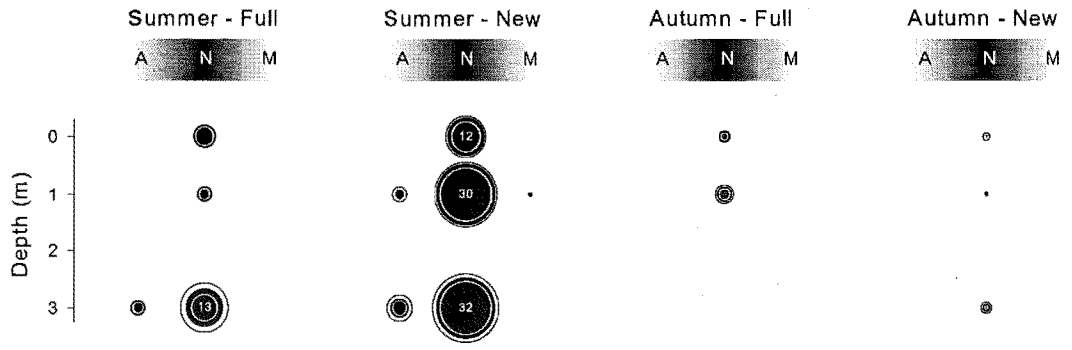

Figure 5.9. The mean abundance ± SE (per 500m^3) of *Acanthoclinus fuscus* larvae found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

A. fuscus larvae appear to undergo nocturnal ascent, with more larvae being found in the uppermost 3 m of water at night than during the day. During summer, most larvae found were at 1 and 3 m in the afternoon, but at night, larvae were found at 0 m as well. Very few larvae of this species were found during the morning tows.

Depth had the single greatest effect on the abundance of unidentified tripterygiid larvae (Table 5.3). Overall, seven times more larvae were found at 3 m than at 0 or 1 m (Fig. 5.10). On average, larvae were five times more abundant at night than during the afternoon or morning. Unidentified tripterygiid larvae were more abundant during a new moon than during a full moon in summer, but not in autumn.

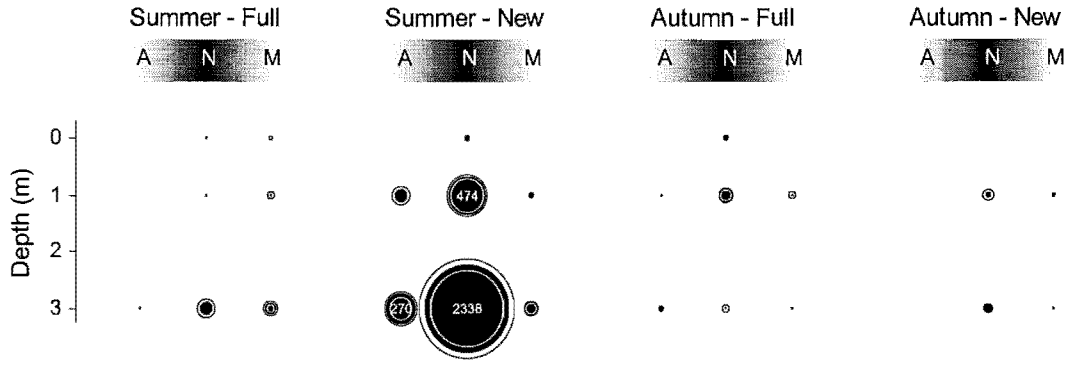

Figure 5.10. The mean abundance ± SE (per 500m^3) of unidentified tripterygiid larvae found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

Unidentified tripterygiid larvae appear to undergo nocturnal ascent, with more larvae being found in the uppermost 3 m of water at night than during the day.

Time had the single greatest effect on the abundance of *Forsterygion lapillum* larvae (Table 5.3). Overall, approximately twenty times more larvae were found at night than during the afternoon or morning (Fig. 5.11). However, this pattern was not evident during a full moon in autumn. On average, fewer larvae were found at 0 m than at 1 or 3 m, but this pattern was less evident at night.

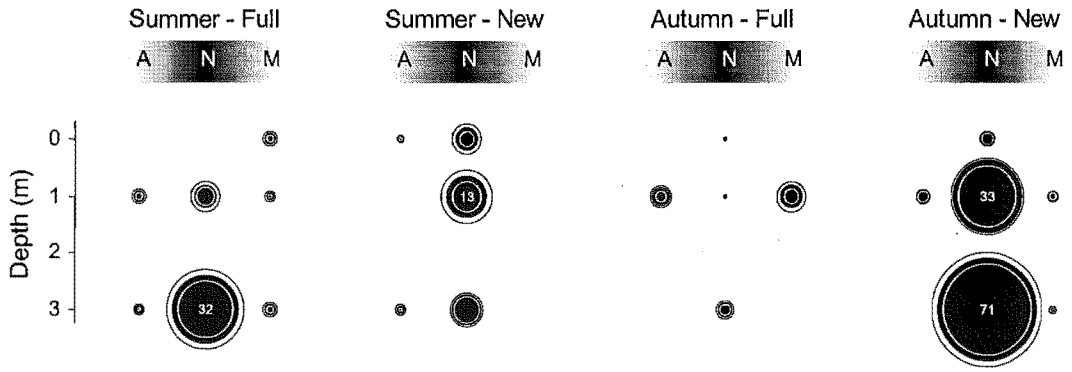

Figure 5.11. The mean abundance ± SE (per 500m^3) of *Forsterygion lapillum* larvae found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

F. lapillum larvae appear to undergo nocturnal ascent, with more larvae being found in the uppermost 3 m of water at night than during the day. Very few larvae were found at 0 m during daytime tows.

Time had the single greatest effect on the abundance of *Forsterygion varium* larvae (Table 5.3). *F. varium* larvae were ten times more abundant at night than during the afternoon or morning, but this was more evident during a new moon (Fig. 5.12). Overall, more larvae were found at 3 m than 0 or 1 m.

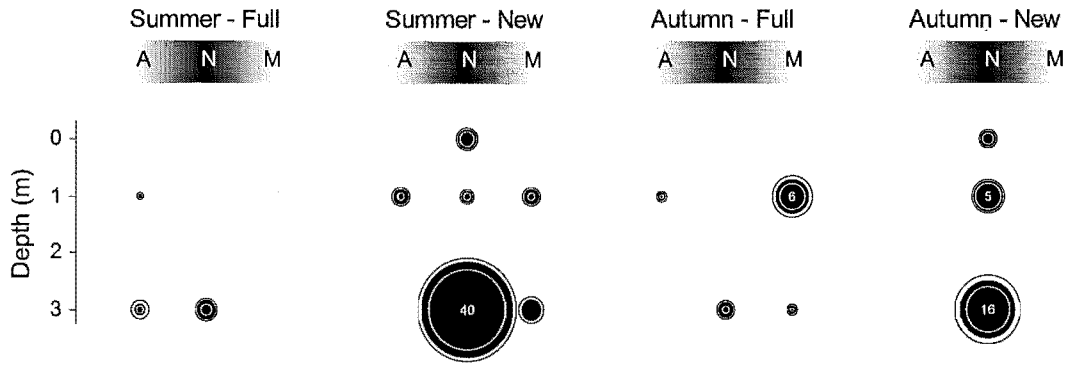

Figure 5.12. The mean abundance ± SE (per 500m^3) of *Forsterygion varium* larvae found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

F. varium larvae appear to undergo nocturnal ascent, with more larvae being found in the uppermost 3 m of water at night than during the day. Larvae of this species were only found at 0 m at night during a new moon and none were found shallower than 3 m at night during a full moon.

Time had the single greatest effect on the abundance of *Gilloblennius tripennis* larvae (Table 5.3). Larvae were twice as abundant during the afternoon and morning as during the night, but this was dependent on the season and on the phase of the moon (Fig. 5.13). Overall, *G. tripennis* larvae were twice as abundant during summer as during autumn.

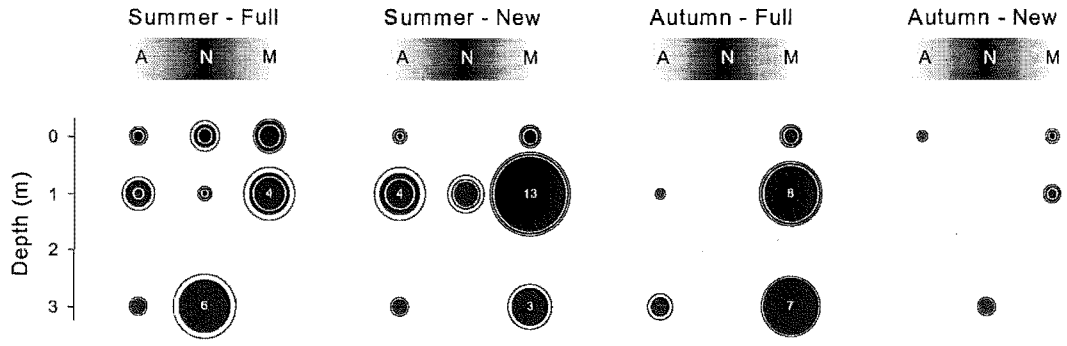

Figure 5.13. The mean abundance ± SE (per 500m^3) of *Gilloblennius tripennis* larvae found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

The diel vertical migration pattern of *G. tripennis* larvae is unclear. During autumn, they appear to undergo nocturnal descent, with less larvae being found in the uppermost 3 m of water at night than during the day. However, this pattern is less evident in summer, particularly during a full moon.

Season had the single greatest effect on the abundance of *Grahamina capito* larvae (Table 5.3). Larvae were thirty times more abundant during summer than during autumn (Fig. 5.14). Overall, very few larvae were found at 0 m, particularly at night. There was no difference between phases of the moon in the average number of *G. capito* larvae found in the tows.

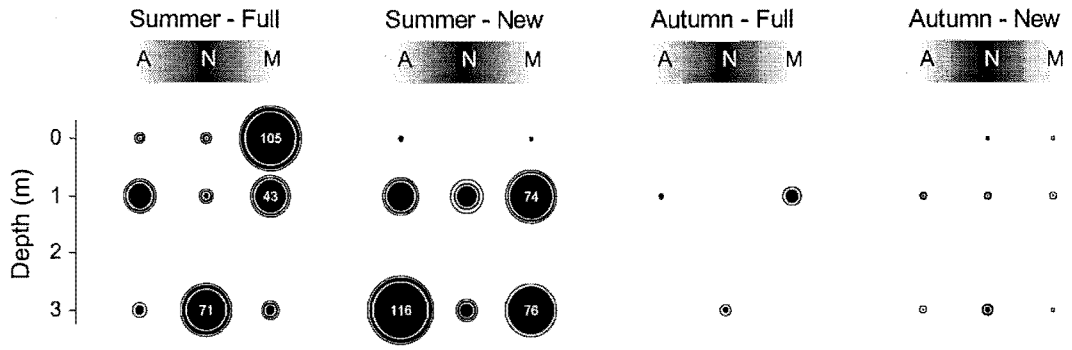

Figure 5.14. The mean abundance ± SE (per 500m^3) of *Grahamina capito* larvae found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

G. capito larvae appear to undergo nocturnal descent, with fewer larvae being found in the uppermost 3 m of water at night than during the day. During the afternoon, most larvae are found at 1 and 3 m, but at night the abundance of larvae at these depths decreases.

Time had the single greatest effect on the abundance of *Ruanoho decemdigitatus* larvae (Table 5.3). Larvae were ten times more abundant at night than during the afternoon or morning, but this pattern was less evident during autumn when significantly fewer larvae were found (Fig. 5.15).

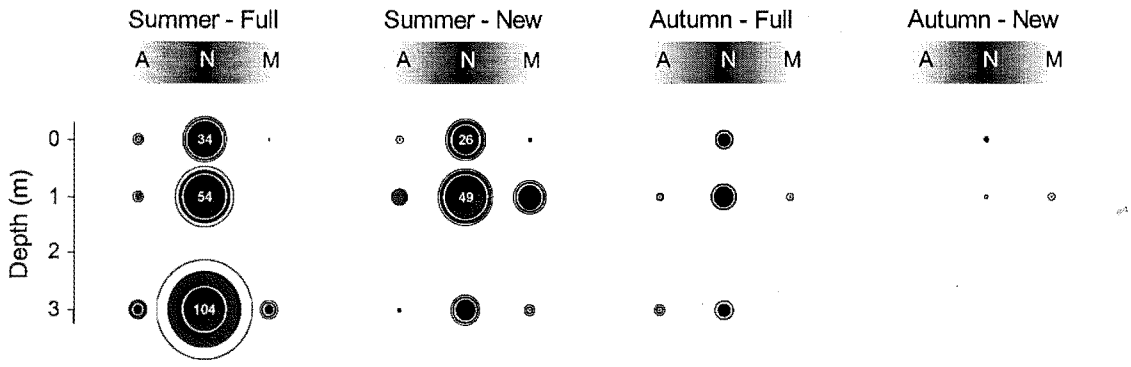

Figure 5.15. The mean abundance ± SE (per 500m^3) of *Ruanoho decemdigitatus* larvae found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

R. decemdigitatus larvae appear to undergo nocturnal ascent, with more larvae being found in the uppermost 3 m of water at night than during the day. *R. decemdigitatus* larvae are less common in the uppermost 3 m of water during a new moon in summer and autumn.

Time had the single greatest effect on the abundance of *Grahamichthys radiata* larvae (Table 5.3). Overall, larvae were three times more abundant at night than during the afternoon or morning (Fig. 5.16). On average, more larvae were found during autumn, particularly during a full moon. Overall, five times more larvae were found during a new moon than a full moon. Fewer larvae were found at 0 m than 1 or 3 m during the afternoon and night. No *G. radiata* larvae were found during the morning tows.

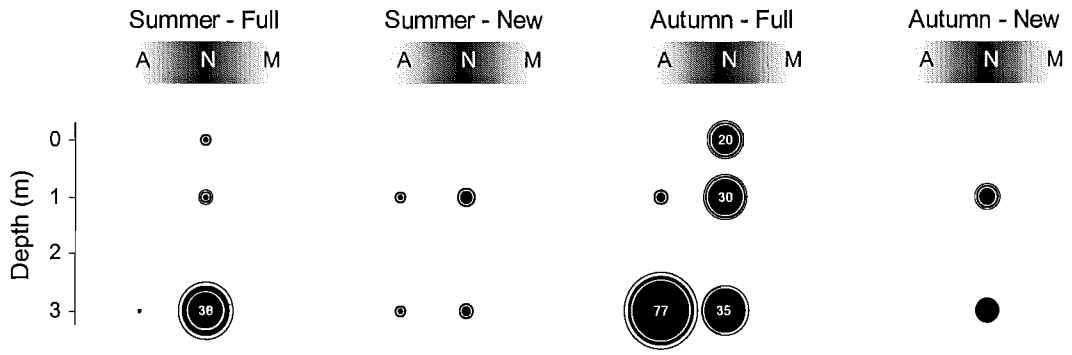

Figure 5.16. The mean abundance ± SE (per 500m^3) of *Grahamichthys radiata* larvae found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

G. radiata appear to undergo nocturnal ascent, with more larvae being found in the uppermost 3 m of water at night than during the day. During the afternoon, most *G. radiata* larvae were found at 1 and 3 m, but at night, larvae were also found at 0 m.

Season and moon phase greatly affected the abundance of *Arnoglossus scapha* larvae (Table 5.3). Larvae were fifty times more abundant during autumn than summer, and only three larvae were found during a new moon (Fig. 5.17). Only two larvae were found during the morning tows.

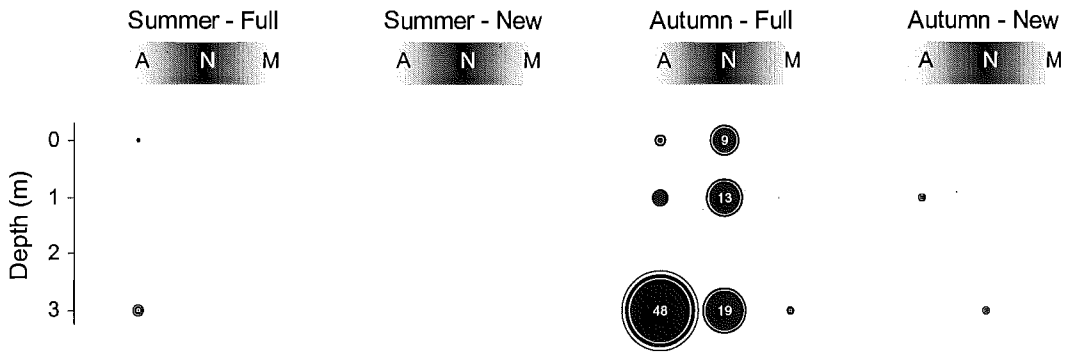

Figure 5.17. The mean abundance ± SE (per 500m^3) of *Arnoglossus scapha* larvae found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

A. scapha appear to undergo nocturnal ascent, with more larvae being found in the uppermost 3 m of water at night than during the day. During the afternoon, most *A. scapha* larvae were found at 3 m, but at night, increased numbers of larvae were found at 0 and 1 m.

Time had the single greatest effect on the abundance of *Rhombosolea plebeia* larvae (Table 5.3). Larvae were eight times more abundant at night than during the afternoon or morning (Fig. 5.18). Overall, four times as many *R. plebeia* larvae were found during a full moon as during a new moon, but this pattern was less evident during autumn.

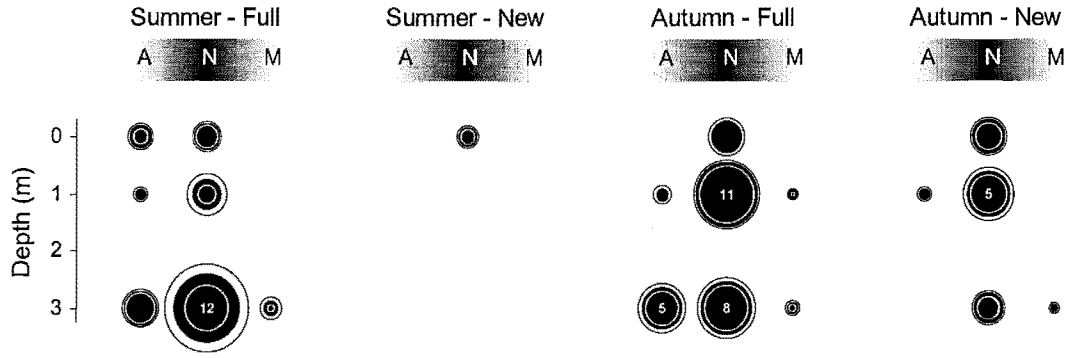

Figure 5.18. The mean abundance ± SE (per 500m^3) of *Rhombosolea plebeia* larvae found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean abundance (white text).

R. plebeia larvae appear to undergo nocturnal ascent, with more larvae being found in the uppermost 3 m of water at night than during the day. During the afternoon, most larvae were found at 1 and 3 m (particularly in autumn), but at night larvae were also found at 0 m. Only eight larvae of this species were found during the morning tows.

Several of the fifteen common taxa were highly correlated (Table 5.4). In examining the overall similarity of samples, there were discrete clusters identified from a PCA (Fig. 5.19). The PCA bi-plot can be interpreted by drawing a line through each taxon point and the origin (0,0). This line is then the imaginary axis for that taxon. When the thirty-six pooled samples are projected onto this axis, those whose projection point is closest to the taxon point contained the highest abundance of that particular taxon. Similarly, the projection points of other taxa onto the imaginary axis will yield a ranking of correlations with the taxon that forms the imaginary axis. In this ranking, the origin indicates zero correlation.

Each of the four clusters (Fig. 5.19) represents a different temporal or spatial pattern. *G. capito* and *G. tripennis* (Graha and Gillo) were more abundant during the afternoon and morning in summer and autumn. *F. lapillum* and *F. varium* (F.lapi and F.vari) were more abundant in samples taken during a new moon at night in summer and autumn. Unidentified retropinnids (Retro) were more common during the afternoon and morning in autumn only. Unidentified tripterygiids, *A. fuscus*, *D. puniceus*, *T. melobesia* and *R. decemdigitatus* (Tript, Acant, Diplo, Trach and Ruano) were most abundant at night during summer. *G. radiata*, *Sprattus* spp., unidentified scorpaenids, *R. plebeia* and *A. scapha* (G.radi, Sprat, Scorp, Rhomb and Arnog) were more abundant during a full moon at night and at 3 m during the afternoon in autumn.

Table 5.4. Pearson correlation coefficients for the fifteen common taxa using thirty-six pooled abundances. Data were log (x+1) transformed prior to correlation analysis. Significant correlations are shown in bold. α level has been corrected for multiple comparisons: ($\alpha = \frac{0.05}{105} = 0.00476$, $r_{0.00476(2),34} = 0.552$).

	Retropinnids	*Diplocrepis puniceus*	*Trachelochismus melobesia*	Unidentified Scorpaenids	*Acanthoclinus fuscus*	Unidentified Tripterygiids	*Forsterygion lapillum*	*Forsterygion varium*	*Gilloblennius tripennis*	*Grahamina capito*	*Ruanoho decemdigitatus*	*Grahamichthys radiata*	*Arnoglossus scapha*	*Rhombosolea plebeia*
Sprattus spp.	0.121	0.515	0.484	**0.609**	0.324	0.375	0.369	0.267	-0.200	-0.267	0.288	**0.850**	**0.671**	**0.717**
Retropinnids		-0.082	0.188	-0.039	-0.274	-0.068	0.149	0.060	-0.196	-0.274	-0.318	0.068	0.255	0.023
Diplocrepis puniceus			**0.647**	0.105	**0.756**	**0.707**	0.522	0.396	-0.073	0.155	0.362	**0.596**	0.001	0.233
Trachelochismus melobesia				0.149	0.543	**0.698**	0.456	0.392	-0.176	0.027	0.277	0.513	0.144	0.288
Unidentified Scorpaenids					0.120	0.182	0.098	-0.010	0.029	-0.167	0.473	0.523	**0.669**	**0.626**
Acanthoclinus fuscus						**0.670**	0.455	0.408	0.003	0.226	**0.719**	0.486	-0.102	0.223
Unidentified Tripterygiids							0.473	0.546	0.169	0.464	0.545	**0.579**	0.073	0.191
Forsterygion lapillum								**0.617**	-0.096	0.326	0.269	0.405	-0.138	0.376
Forsterygion varium									0.137	0.298	0.251	0.270	-0.109	0.176
Gilloblennius tripennis										0.528	0.155	-0.112	-0.273	-0.240
Grahamina capito											0.308	0.010	-0.415	-0.209
Ruanoho decemdigitatus												0.471	0.083	0.417
Grahamichthys radiata													**0.607**	**0.673**
Arnoglossus scapha														**0.556**

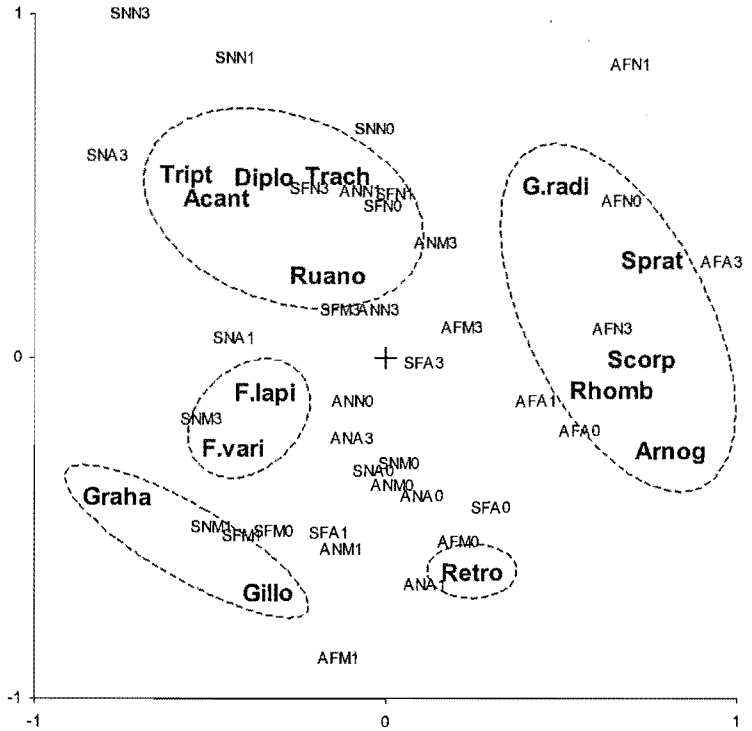

Figure 5.19. Correlation bi-plot based on Principle Components Analysis of the total abundance data. Taxa codes are the first five letters of the genus or family of the fifteen common taxa. Sample codes indicate season/moon phase/time/depth. Dotted ellipses contain positively correlated taxa.

Time had the single greatest effect on the volume of zooplankton (Table 5.3). Overall, the volume of zooplankton was five times greater at night than during the afternoon or morning (Fig. 5.20). More zooplankton were found at night during a new moon in summer than during a full moon, but this pattern was not evident in autumn.

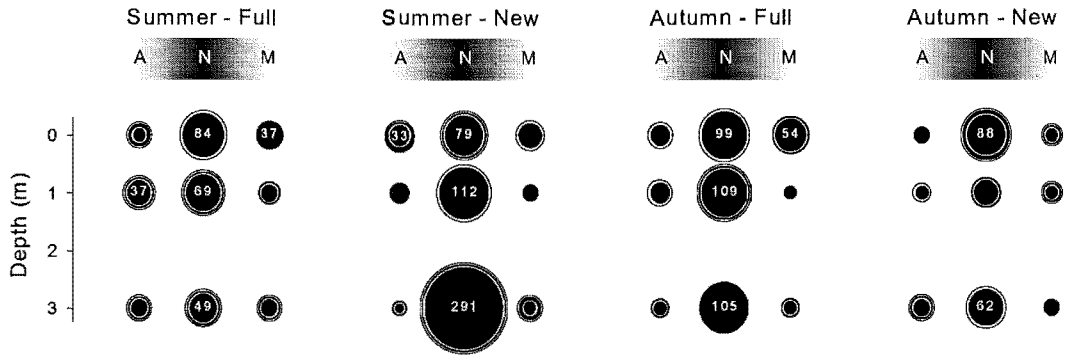

Figure 5.20. The mean volume (ml) ± SE (per 500m^3) of zooplankton found at three depths (0, 1 and 3 m), during the afternoon (A), night (N) and morning (M), during two seasons and two phases of the moon. The SE is shown as a black ring outside of (+) and a white ring inside of (-) the mean (black disc). The disc area is proportional to the mean volume (white text).

Many species of zooplankton appear to undergo nocturnal ascent, with a greater volume of zooplankton being found in the uppermost 3 m of water at night than during the day. Although not quantified, there was a very noticeable increase in the abundance of euphausiids (mainly *Nyctiphanes australis*), cephalopods (mainly *Sepioloidea pacifica*), amphipods and copepods in the night samples. Zooplankton volumes were relatively uniform over the three depths on most occasions, indicating little stratification in the uppermost 3m of water.

5.4 DISCUSSION

It is clear from this study, and from the results of Chapter 4, that larval fish in even relatively shallow water can have finely stratified vertical distributions. The distribution of larval fish was not uniform over the three depths that were sampled, with most common taxa showing some degree of vertical stratification. Significant differences in the abundance of all common taxa were found among depths, even over the relatively small vertical distance of 3 m. This is consistent with studies elsewhere that have reported vertical stratification for larval fish assemblages in shallow coastal waters (Ahlstrom 1959, Brewer & Kleppel 1986, Kingsford 1986, Leis 1991b, Gray 1996, 1998). Kingsford (1986) found that larval fish were vertically stratified in water columns of any depth, even in waters as shallow as 1 m.

Any large differences in the abundance of fish larvae over relatively small vertical distances are likely to be the result of steep gradients in physical, chemical or biological parameters. A water column that has a complex structure in the vertical dimension usually produces a planktonic system that is more complex on the vertical plane than on the horizontal plane (Röpke 1993). This complexity is increased by active vertical movements of planktonic animals in response to those gradients.

It has been suggested that physical stability in the water column is critical for the maintenance of the vertical distribution of larval fish (Lasker 1975, 1981). However, wave action and turbulence in my study area probably produced a mixed surface layer and prohibited thermal stratification. The vertical stratification of larval fish distributions in this mixed layer would be consistent with the findings of Gray (1996, 1998) who reported that thermal stratification of the water column is not a prerequisite for vertical stratification of fish larvae.

The vertical distribution of many of the common taxa changed markedly with the time of day. Most of the common taxa were more abundant at 1m and 3 m during the day than they were at the surface. Relatively few *Sprattus* spp., retropinnid, *D. puniceus*, *T. melobesia*, *A. fuscus*, unidentified tripterygiid, *F. lapillum*, *F. varium*, *G. radiata* and *A. scapha* larvae were found at the surface (0 m) during the day, but in most cases these taxa were very abundant at either 1m, 3 m or both. However, the vertical distribution of these taxa changed markedly at night. Many more larvae from each of these taxa, except the retropinnids, were found in the uppermost 3 m of the water column at night. Furthermore, taxa that were not found at the surface during the day were found often in large numbers at night. Taxa that showed an increased abundance in the uppermost 3 m of the water column at night are likely to have made a 'nocturnal ascent' type vertical migration (Smith *et al.* 1978, Perry & Neilson 1988) (Table 5.5).

Table 5.5. Vertical migration patterns of the fifteen common taxa from this study.

Nocturnal Ascent	Nocturnal Descent	None/Unclear
Sprattus spp.	Retropinnids	*T. melobesia*
D. puniceus	*G. capito*	*G. tripennis*
Scorpaenids		
A. fuscus		
Unidentified tripterygiids		
F. lapillum		
F. varium		
R. decemdigitatus		
G. radiata		
A. scapha		
R. plebeia		

Only two of the common taxa appeared to have a 'nocturnal descent' type vertical migration pattern (Yamashita *et al.* 1985, Lyczkowski-Schultz & Steen 1991) (Table 5.5). Although retropinnid and *G. capito* larvae were most common during different seasons, fewer larvae from both taxa were found in the uppermost 3 m of the water column at night than during the day. Neither of these taxa was consistently abundant at 0 m at any time of the day.

Nocturnal descent has been termed "reverse diel vertical migration" and has been observed in the larvae of a wide range of fish species (Ryland 1964, Wood 1971, Ohman *et al.* 1983, Boehlert *et al.* 1985, Yamashita *et al.* 1985, Leis 1986, Sogard *et al.* 1987, Lyczkowski-Schultz & Steen 1991, Haldorson *et al.* 1993, Brodeur & Rugen 1994). However, in their review Neilson & Perry (1990) found this pattern of diel vertical migration to be less common than nocturnal ascent. Yamashita *et al.* (1985) suggested that feeding activity may play an important role in initiating nocturnal descent. Japanese sand-eel larvae feed in the upper levels of the water column during the day, but when feeding stops at night the larvae stop swimming and

sink. The authors suggested that nocturnal inactivity in sand-eel larvae could reduce predation pressure in two ways: first by reducing the probability of attack by predators that detect the vibrations of their prey (e.g. chaetognaths) and second by removing the larvae from the upper water layer where predators are concentrated at night.

T. melobesia and *G. tripennis* were the only common taxa that did not appear to have any consistent vertical migration patterns. *T. melobesia* larvae appeared to ascend nocturnally in summer, but not in autumn. *G. tripennis* larvae appeared to descend nocturnally on some occasions, but not during others. These taxa may not have a consistent vertical migration pattern, or they may repetitively rise and sink during the night thereby producing a vertical distribution that appears confused. This highlights one of the difficulties of studying vertical migrations of fish larvae at the population level; at any moment in time different larvae may be at different stages of sinking and rising (Pearre 1979, Haney 1988). Sampling at the population level masks the behaviour of individual larvae, assumes all larvae are behaving the same and are in synchrony, and assumes there are no ontogenetic differences in vertical distribution (cf. Leis 1991b, Kendall *et al.* 1994). Observations of the movements of individual fish larvae (similar to those of Leis *et al.* 1996) may be required to fully understand patterns of diel change in vertical distributions (Gray 1998).

Diel changes in the vertical distribution of larval fish populations have been described for many species in many regions (see review by Neilson & Perry 1990). The widespread occurrence of diel vertical migration suggests that there are adaptive advantages associated with this behaviour. The adaptive significance of these migrations is still in dispute, but current hypotheses are centred around predator avoidance and optimal foraging arguments (Kerfoot 1985, Fortier & Harris 1989, Lampert 1989, Heath 1992). These hypotheses predict that fish larvae migrate deeper into the water column during the day to avoid predation, but return to the surface at night to utilise the abundant food supply.

While vertical migration by fish larvae to avoid predators has been suggested in many studies (see review by Frank & Leggett 1985), there are several reasons to suppose that it is neither a universal nor complete explanation. First, there is sufficient light at the daytime residence depths of many migrants for predators to function successfully (Clarke 1936). Second, many potential predators are also strongly migratory (Longhurst 1976, Bulman & Blaber 1986). Third, vertical migration may put larval fish at a greater risk of predation if they migrate into deeper strata which are already occupied by potential predators (Bailey 1989).

It is not possible to tell from this study why the common taxa migrated vertically. Although there was a marked increase in the abundance of potential food (copepods) at the surface at night, there also appeared to be an increase in potential predators (euphausiids, amphipods and chaetognaths). Therefore, a nocturnal ascent that would appear to be advantageous in terms of food supply may be disadvantageous because of an increased risk of predation. Conversely, taxa that descended nocturnally (retropinnids and *G. capito)* may lower their risk of predation, but are likely to encounter sub-optimal food supplies. Without more detailed knowledge of the diel vertical distribution of zooplankton in the Kaikoura region it is not possible to determine the cause of the apparent vertical migration.

It is important to recognise that the results of this study may be influenced by the ability of larger larvae to avoid capture, especially during daylight hours. While avoidance can be reduced by using a net with a large mouth, by removing bridles and tow lines from immediately in front of the mouth of the net and by towing the net at higher speeds (Clutter & Anraku 1968), as was done in my study, it can never be eliminated. Although it is possible that net avoidance could account for some of the differences in abundance seen between night and day, it seems highly unlikely that all of the differences observed (e.g. increases from a mean of 270 to 2338 tripterygiid larvae per 500 m^3) could be explained by daytime avoidance alone. Furthermore, the vertical distribution of taxa that showed greater abundances near the surface during the day than at night (retropinnids and *G. capito*) could not be the result of net avoidance.

The narrow depth range that was sampled in this study may misrepresent diel changes in the vertical migration of larval fish. Although an increased abundance in the uppermost 3 m of the water column at night may be indicative of vertical migration, it may also be the result of a breakdown in vertical structure at night. Several authors have reported a weakening in vertical stratification among larval fish at night in shallow temperate waters (Brewer & Kleppel 1986, Leis 1991b, Gray 1998). This pattern of dispersion at night in shallow waters may be in response to the loss of the light stimulus that regulates daytime vertical distribution (Leis 1991b).

The degree of nocturnal ascent by some taxa appeared to be influenced by ambient light levels. *F. lapillum* and *F. varium* larvae were more abundant at night in the uppermost 3 m of the water column. In addition, both of these taxa were more abundant during new moon nights than full moon nights. Other taxa (Scorpaenids, *R. decemdigitatus* and *G. radiata*) appeared to be more abundant during full moon nights when ambient light levels were considerably higher.

Light intensity is the major factor that triggers the vertical migration of fish larvae in laboratory studies (Woodhead & Woodhead 1955, Blaxter 1973) and seems to be responsible for much of the observed variability in distribution and migration patterns (Röpke 1993). Blaxter & Hunter (1986) observed that clupeoid fish are more abundant at the surface during nights when the ambient light levels are lowest. Russell (1926) found that Callionymidae larvae did not ascend nocturnally on "moonlight" nights, whereas their distribution stretched upwards to the surface on "dark" nights. Kingsford (1986) suggested that the migration of larval fish into surface waters in northeastern New Zealand may be reduced when ambient light is high.

Kingsford (1986) completed the only other comparative study in New Zealand of the vertical distribution of larval fish during the day and night. However, the taxa that dominated his study in north-eastern New Zealand (*Sardinops neopilchardus*, *Engraulis australis*, *Trachurus* spp., *Chrysophrys auratus* and *Scomber australasicus*) were not found in my study. Larvae of the pilchard, *S. neopilchardus,* are closely related and morphologically very similar to those of sprat (*Sprattus* spp. in my study) (Baker 1972). The increased abundance of *Sprattus* spp. larvae in the uppermost 3 m of the water column at night in my study is consistent with Kingsford's (1986) observations for *S. neopilchardus* and with several other studies that have reported high densities of clupeoid larvae near the surface at night (Russell 1926, 1928, Hunter & Sanchez 1976, Blaxter & Hunter 1982).

Chapter Six

Two Methods for Sampling Larval Fish in Inshore Temperate Waters

6.1 INTRODUCTION

Because the successful completion of the pelagic phase of marine teleost fishes is crucial to subsequent fish populations, there has been considerable research on ichthyoplankton and the processes influencing survival and settlement of fish larvae from the open water community. A large portion of this work involves sampling and development of appropriate techniques to determine species composition and size classes of the ichthyoplankton in different environments. Although methods and equipment for sampling ichthyoplankton in open water are well developed, usually involving towing multiple plankton nets from large research vessels, most are not practicable for sampling in shallow inshore waters, particularly near rocky reefs. Many methods have been used for sampling ichthyoplankton close to reefs, including diver-guided plankton nets (Brogan 1994b), moored nets (Kingsford & Finn 1997), purse seines (Kingsford & Choat 1985), plankton pumps (Powlik *et al.* 1991), visual censuses (Kingsford & Choat 1989), aggregation devices that attract fish into collection sites (Victor 1991) and light traps (Doherty 1987). However, it is clear that different methods usually sample different components of the ichthyoplankton and the usefulness of each method is related to environmental conditions or types of habitat.

Light traps are useful passive devices for sampling larval fishes in marine habitats and have been instrumental in understanding larval abundance patterns along the Great Barrier Reef (Milicich & Doherty 1994, Thorrold & Williams 1996). However, only two studies, both done in the tropics, have compared the performance of light traps with plankton nets, which are extensively used for sampling ichthyoplankton in marine waters. Light traps have rarely been used in temperate areas and it is not known how useful they are in sampling the larval fish community in these less diverse regions. For example, the cold, murky waters of southern New Zealand support only ca. 70 species of coastal fishes while the Great Barrier Reef supports more than 1500 fish species. Both the lower diversity and poorer water clarity of temperate waters is likely to affect the sampling properties of light traps and may limit their usefulness in these areas.

Light traps exploit the positive phototactic response of larval and juvenile fishes. Therefore, their success depends on the ability of larvae to see a light, to swim towards it and enter an illuminated enclosure (Brogan 1994b), all of which may change during ontogeny (Bulkowski & Meade 1983) or with light intensity and wavelength (Gehrke 1994). It is generally accepted that light traps are both species- and size-selective (Gregory & Powles 1985, 1988, Doherty 1987, Thorrold 1992, 1993, Choat *et al.* 1993, Brogan 1994b) and, therefore, it is necessary to determine the sampling properties of light traps before incorporating them into a sampling design.

The purpose of this study was to compare light traps and plankton nets for sampling the inshore larval fish community. My general question was whether these two methods yielded the same taxonomic composition, relative abundance of taxa, and size frequency of fish larvae. Because the ichthyoplankton can vary seasonally, with the phase of the moon and by habitat, these factors were incorporated into the sampling design. Therefore, I posed as null hypotheses: that the light trap and plankton net samples would be identical in two inshore habitats, two seasons and two moon phases.

6.2 METHODS

6.2.1 Study area

Sampling was done at two sites on the southern side of the Kaikoura Peninsula (Fig. 6.1). The first site (reef habitat) had a rocky reef substrate with dense beds of macroalgae (predominately *Marginariella boryana* and *Carpophyllum maschalocarpum*) and a mean depth of 4.2 m. It was interspersed with deep channels (maximum depth 9 m) and rocky pinnacles. The second site (beach habitat) was adjacent to a fine shingle beach (5-10mm particle diameter), was free of macroalgae and was situated over a gently sloping sandy substrate. It had a mean depth of 4.5 m and a maximum depth of 8 m. The nearest rocky reef was ca. 100 m alongshore. The two sites were separated by rocky promontories and a distance of 1.6 km

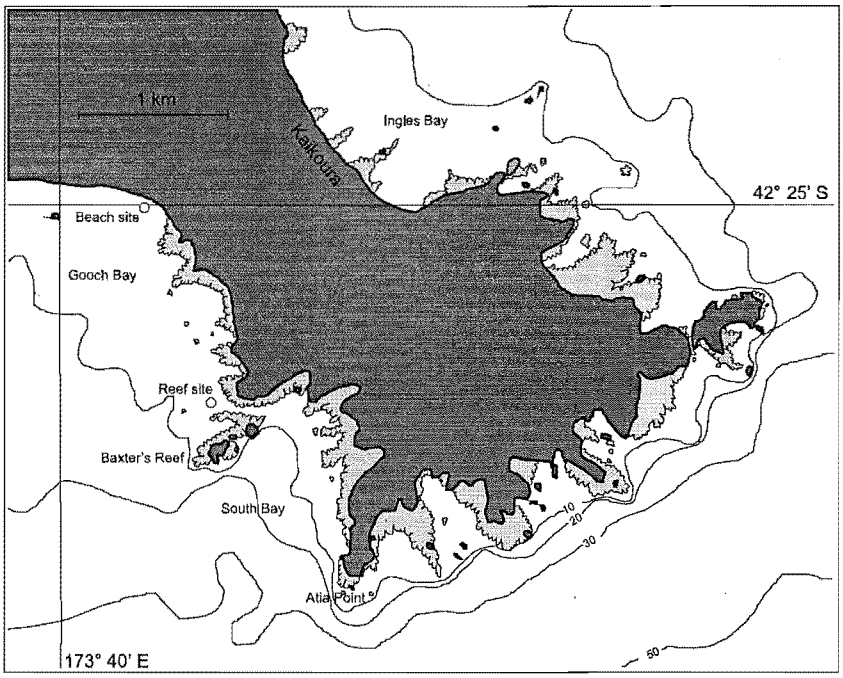

Figure 6.1. Map of the Kaikoura Peninsula on the northeast coast of the South Island. The beach and reef habitat sampling sites are shown. Bathymetry is in metres.

6.2.2 Sampling gear

I constructed light traps that were a modified version of those described by Doherty (1987). The body of the light trap (Fig. 6.2) was made from a 240 litre mobile plastic waste bin (Sulo, Australia), divided by two opaque partitions into three chambers. Three sides of the upper chamber were fitted with clear plastic windows (290 x 190 mm) each containing two moulded entrance slots. Each horizontal slot tapered from 60 x 300 mm down to 12 x 250 mm. The partitions separating the chambers contained two identical slots. The middle chamber had no external entrance slots but was fitted with a 250 x 300 mm clear plastic window. The lower chamber was fitted with 0.5 mm stainless steel mesh panels (240 x 150 mm) on three sides and a 50 mm drain hole (closed with a rubber stopper).

A central waterproof core ran through all three chambers. The upper section of the core was constructed from 150 mm wastepipe and contained a rechargeable lead-acid battery (12v 10Ah) and a digital timing mechanism. The lower section of the core was constructed from 40 mm clear plastic tube and contained the three light sources (6 W fluorescent tubes). Each of the

light sources was contained solely within a chamber. The timer mechanism was identical to that described by Doherty (1987) with the light in the lower chamber remaining lit throughout the sampling sequence and the lights in the upper and middle chambers alternating at 5 min intervals.

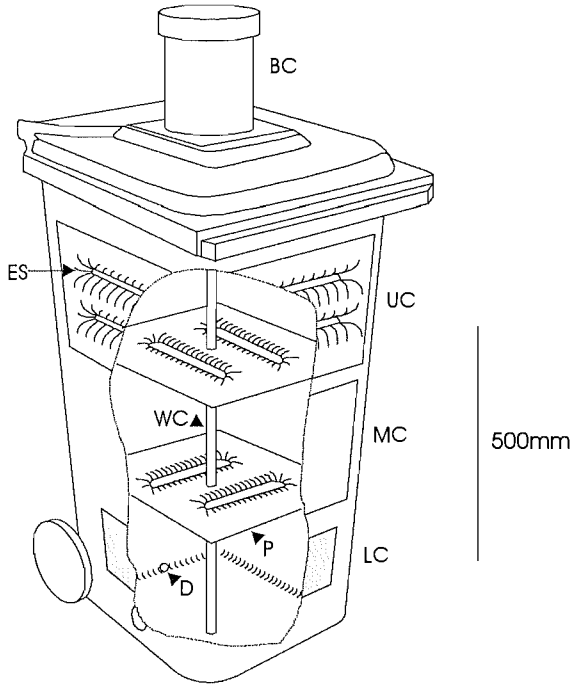

Figure 6.2. Diagram of a light trap with the side partially cut away. BC: battery chamber; UC: upper chamber; MC: middle chamber; LC: lower chamber; P: partition; D: drain; WC: waterproof core; ES: entrance slot.

The plankton net had a 707 x 707 mm mouth (0.5 m^2) and 280 µm mesh. The net was a box-pyramid design with a filtration efficiency of 1:11. A General Oceanics digital flowmeter (Model 2030R) was fitted in the mouth of the net (at 0.33 of the net width) to determine the volume of water filtered per tow. The net was towed with a four-point bridle alongside a 6m boat. The net was rigged so that it sampled with the uppermost edge of the mouth of the net at a fixed depth of 1 m and was towed for 5 min at a speed of ca. 1 ms^{-1}.

6.2.3 Sampling procedure

The reef and beach habitats were sampled on two nights during both a new moon (30th January 1997 and 3rd February 1997) and a full moon (17th February 1997 and 21st March 1997) in summer. This sampling design was repeated during a new moon (31st March 1997 and 2nd April 1997) and a full moon (15th April 1997 and 17th April 1997) in autumn. On each night, the two different sampling methods were deployed in both habitats. The two habitats were sampled in random order using the following method: two hours after dusk, three automated light traps were deployed. Each light trap was suspended below an anchored buoy so that the entrance slots into the light trap were 1.5 m below the surface. The light traps were positioned ca. 15 m apart. The three light traps were programmed to start simultaneously, sample for 30 min and then shut down. The light traps were left in the water for no more than one hour in total. While the light traps were sampling, three replicate tows were made nearby with the plankton net. All tows were completed approximately 100 m from the anchored light traps and filtered 138 - 218 m^3 of water per tow.

After the completion of each sample, the plankton net and light traps were washed thoroughly with pumped seawater and the sample was fixed in buffered 10% formalin in seawater. All fish larvae were removed from the samples using a dissection microscope, identified to the lowest possible taxonomic level, and stored in buffered 2% formalin in freshwater. All fish (except those that were badly damaged) were measured to the nearest 0.5 mm by placing them on a graduated slide. Notochord length was measured for preflexion and flexion larvae, and standard length was measured for postflexion larvae. For light traps, abundance is given as the number of fish per sample. Plankton net samples were standardised to the number of fish per 200 m^3.

6.2.4 Analysis

Two types of data were collected. Both plankton nets and light traps collected a wide range of species allowing tests of species richness between sampling procedures. Because all undamaged fish larvae were measured, sizes could be compared for larval fish captured by the two sampling methods across seasons, phases of the moon and habitat. Abundances of larval fish, comparing the two sampling methods and their interactions with other factors, could not be tested because the volume of water sampled by light traps for each species is unknown. However, a correlation coefficient was calculated for the abundance of each taxon in the samples from the two methods by summing the abundance of individual taxa across the three replicates on each sampling occasion and correlating this total with the total obtained from the other sampling method.

The size-frequency distributions of fish larvae caught by the plankton nets and light traps were compared using the Kolmogorov-Smirnov (K-S) test. The variables tested were the total fish sample and seven individual taxa, which were selected on the basis of comprising at least 1% of the total catch in either sampling method.

To test the number of taxa caught between light traps and plankton nets across season, moon phase and habitat, a mixed model ANOVA was used with the factors method (light trap and plankton net), season (summer and autumn), moon phase (full and new), nights within season x moon phase (treated as random) and habitat (reef and beach). Prior to ANOVA, the data were tested for homogeneity of variances using Cochran's test. *Post hoc* pooling was used to eliminate non-significant ($p > 0.25$) higher order interactions from the model (Underwood 1997).

Canonical Discriminant Analysis was used to display the relationship between season, moon phase, habitat, method of sampling and the taxonomic composition of the samples. The catch of the light traps could not be standardised because the volume of water sampled was not known. Because of this, the proportional abundance of each taxon in the light trap samples and in the standardised plankton net samples was analysed. However, any taxon that did not comprise at least 1% of the total catch in either sampling method was excluded from further analysis.

6.3 RESULTS

In total, the 96 samples captured 8,086 larval and pelagic juvenile fish from fourteen families. There was a marked difference in the taxonomic composition of the samples taken by the two methods. The plankton net took almost twice as many taxa from twice as many families as the light traps (Table 6.1) and collected a wider size-range of individuals from most taxa (Table 6.2). Overall, the light traps caught far fewer fish larvae than the plankton nets (Table 6.1). However, all light trap and plankton net samples contained fish larvae.

Table 6.1. Number of samples, total individuals, volume of water sampled and taxonomic composition of samples taken by the two sampling methods.

Sampling method	Number of samples	Number of fish	Volume of water sampled (m^3)	Number of taxa	Number of families
Light trap	48	1,589	unknown	12	7
Plankton net	48	6,497	7,880	23	14

Table 6.2. Composition and size range of samples taken by the plankton net and the light traps. Data are pooled across season, moon phase and habitat. Summary of occurrences (Oc), minimum (Min), maximum (Max), and mean ($\bar{x}$) size (mm standard length), total number of individuals (n) within each taxon, and percentage (%) of total catch from 48 light trap samples and 48 plankton net samples.

Family	Taxa	Plankton net						Light traps					
		Oc	Min	Max	$\bar{x}$	n	%	Oc	Min	Max	$\bar{x}$	n	%
Clupeidae	*Sprattus* spp.	47	4.0	44.0	22.3	1663	25.60	14	17.0	67.5	34.5	45	2.83
Retropinnidae	Retropinnidae	28	13.0	61.0	34.6	359	5.53	24	20.5	62.5	35.8	487	30.65
Moridae	*Auchenoceros punctatus*	1	19.5	19.5	19.5	1	0.02	0					
Gobiesocidae	*Diplocrepis puniceus*	16	3.0	5.5	4.9	48	0.74	6	6.0	15.5	12.4	11	0.69
	Trachelochismus melobesia	28	3.0	15.5	6.3	308	4.74	18	3.5	15.5	9.6	28	1.76
	Trachelochismus pinnulatus	5	4.5	5.5	5.0	5	0.08	0					
Trachichthyidae	*Paratrachichthys trailli*	5	11.0	16.0	14.1	12	0.18	4	16.0	16.5	16.2	6	0.38
Scorpaenidae	Unidentified Scorpaenidae	1	2.5	2.5	2.5	1	0.02	0					
	Scorpaena papillosus	5	18.0	22.0	20.3	8	0.12	0					
Acanthoclinidae	*Acanthoclinus fuscus*	4	3.5	11.0	6.5	4	0.06	0					
Mugilidae	*Aldrichetta forsteri*	2	31.0	32.0	31.5	2	0.03	0					
Labridae	*Notolabrus celidotus*	3	10.0	14.5	12.1	4	0.06	0					
Tripterygiidae	Unidentified Tripterygiidae	42	2.0	22.0	12.9	1481	22.80	9	11.5	26.0	18.6	229	14.41
	Forsterygion lapillum	25	14.0	32.5	22.5	241	3.71	27	9.5	29.0	24.5	162	10.20
	Forsterygion varium	34	11.5	39.0	22.0	1317	20.27	32	15.0	33.5	23.5	483	30.40
	Gilloblennius tripennis	15	3.0	17.5	8.7	155	2.39	0					
	Grahamina capito	21	8.5	21.5	14.4	110	1.69	12	7.0	22.5	15.3	93	5.85
	Ruanoho decemdigitatus	22	3.0	26.0	4.5	257	3.96	7	19.5	22.0	20.4	19	1.20
Clinidae	*Cologrammus flavescens*	13	18.5	28.5	21.3	19	0.29	12	18.0	22.0	20.4	23	1.45
Eleotridae	*Grahamichthys radiata*	36	4.5	41.5	18.5	173	2.66	3	17.0	19.0	18.2	3	0.19
Gobiidae	*Gobiopsis atrata*	16	2.5	17.0	3.3	120	1.85	0					
Pleuronectidae	*Peltorhamphus* spp.	2	12.0	13.5	12.5	3	0.05	0					
	Rhombosolea plebeia	37	4.5	9.0	6.7	206	3.17	0					
Total			2.0	61.0	17.8	6497			3.5	67.5	17.9	1589	

Eleven taxa occurred exclusively in the plankton net samples (Table 6.2), but no taxa were caught solely by the light traps. Eight of these eleven taxa were rare, each comprising ≤0.12% of the total plankton net catch. However, the remaining three taxa (*Gilloblennius tripennis*, *Gobiopsis atrata* and *Rhombosolea plebeia*) were relatively common in the plankton net samples, each occurring in at least fifteen of the samples and having more than 100 larvae in total (Table 6.2).

There was little correlation between the abundance of each taxon in the plankton net and light trap samples. Only six (*Sprattus* spp., Retropinnidae, *Trachelochismus melobesia*, *Paratrachichthys trailli*, *Grahamina capito* and *Ruanoho decemdigitatus*) of the 23 taxa collected showed a positive correlation ($p < 0.05$) between the abundance of fish larvae in the plankton net and light trap samples. The remainder showed little correlation or were not collected by the light trap.

In both sampling methods, a few abundant taxa dominated the catch (Table 6.2). The three most abundant taxa collected by the plankton net and light traps accounted for 68.7% and 75.4% of the catch, respectively. The abundance distribution of the plankton net samples was more balanced than that of the light traps. However, the rank of the taxa was very different between sampling methods (Fig. 6.3). For example, *Sprattus* spp. was the most common taxon in the plankton net samples (25.6%), but only the sixth most common in the light trap samples (2.8%). Retropinnidae was the most common taxon in the light trap samples (30.7%), but only the fourth most common in the plankton net samples (5.5%).

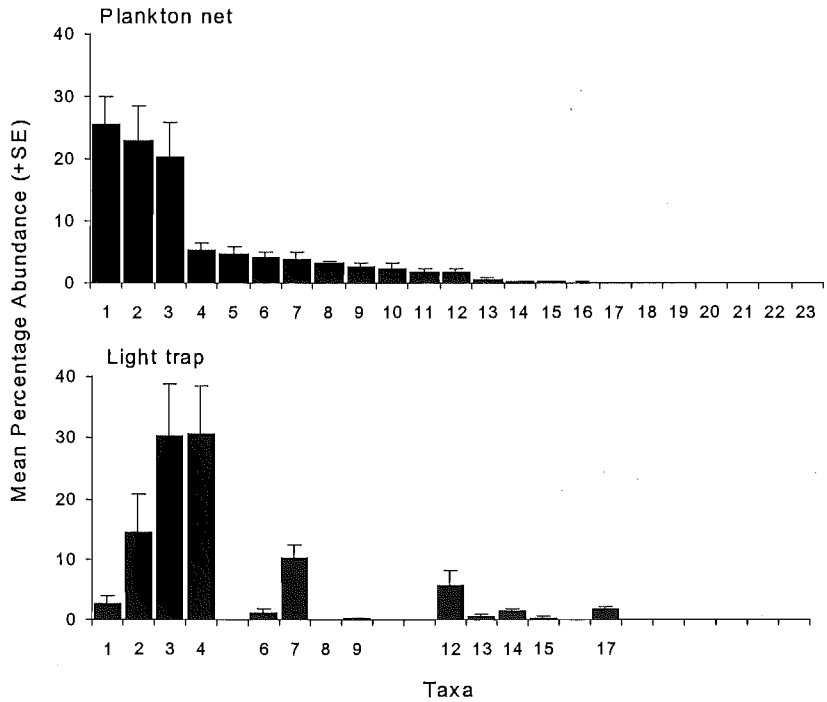

Figure 6.3. Mean percentage abundance (+ SE) and ranked taxonomic category of larval fish collected by the plankton net and the light traps. n = 48. Key to taxa: 1 *Sprattus* spp.; 2 Unidentified tripterygiids; 3 *F. varium*; 4 retropinnids; 5 *T. melobesia*; 6 *R. decemdigitatus*; 7 *F. lapillum*; 8 *R. plebeia*; 9 *G. radiata*; 10 *G. tripennis*; 11 *G. atrata*; 12 *G. capito*; 13 *D. puniceus*; 14 *C. flavescens*; 15 *P. trailli*; 16 *S. papillosus*; 17 *T. pinnulatus*; 18 *A. fuscus*; 19 *N. celidotus*; 20 *Peltorhamphus* spp.; 21 *A. forsteri*; 22 *A. punctatus*; 23 Unidentified scorpaenids.

There were significant differences between the mean standard length of fish captured by the two sampling methods in all taxa tested (Fig. 6.4). For all taxa, larvae collected by the light traps were significantly larger than those in the plankton net samples. The few *Sprattus* spp. captured by the light traps were on average 12 mm larger than those in the plankton net samples. The larger *Sprattus* spp. larvae caught by the light trap were missing from the samples taken by the plankton nets. (Fig. 6.4). The size-frequency distributions of retropinnids caught in the light traps and plankton nets overlap broadly, but there is a slight difference in the modal size class (Fig. 6.4). Only five of the retropinnids caught were < 20mm SL and the majority of fish larvae in samples collected by both methods were > 30 mm SL. When the size-frequency of the total catch from the light traps is compared to that from the plankton net, it is clear that smaller individuals are more common in the plankton net (Fig. 6.4). Fish larvae >40mm, which were relatively common in the light trap samples, were very rare in the plankton net samples.

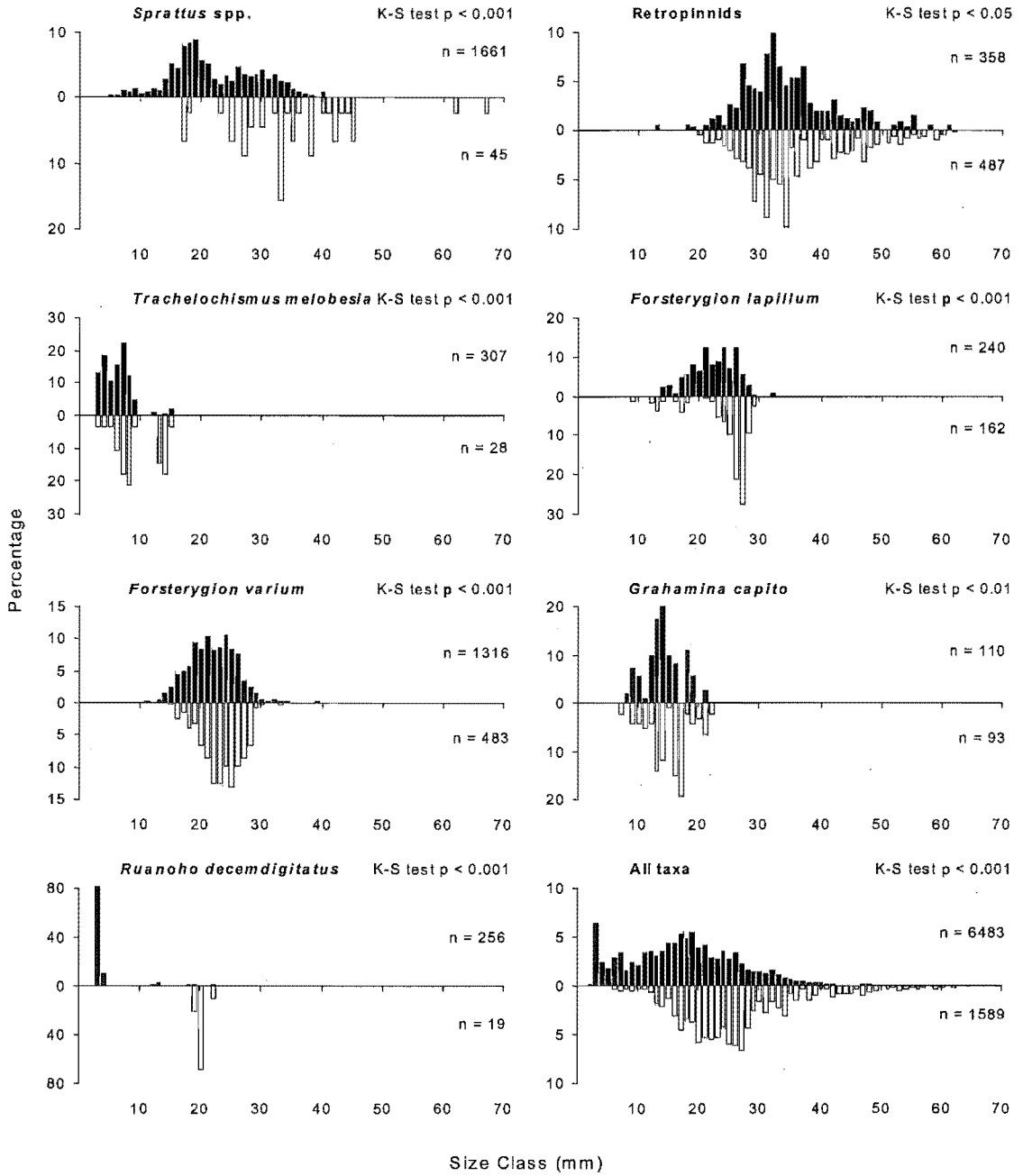

Figure 6.4. Size distributions of fish larvae in the plankton net (solid bars) and light trap (open bars) samples.

The three taxa, *G. tripennis*, *G. atrata* and *R. plebeia*, that were relatively common in the plankton net samples but absent from the light trap samples had very few individuals in the larger size classes (> 10 mm), which comprised the majority of the light trap samples (Fig. 6.5).

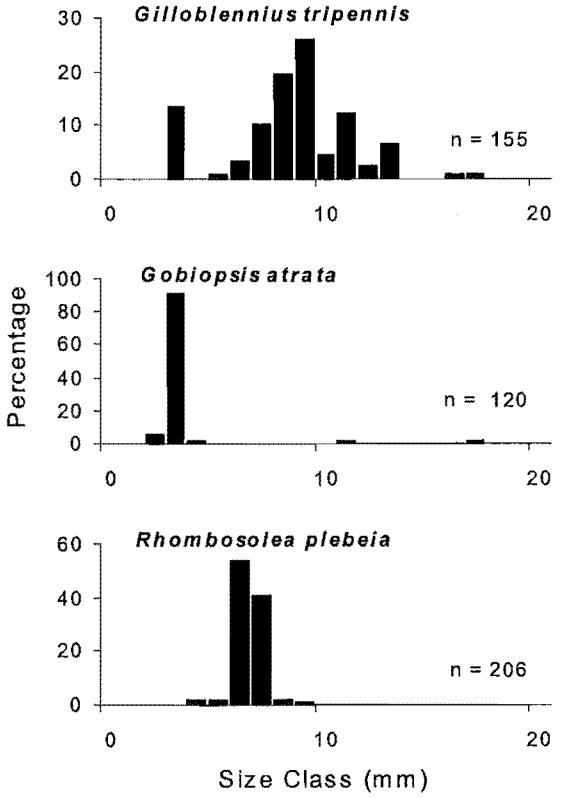

Figure 6.5. Size distributions of larval fish from three taxa that were common in plankton net samples, but absent from light trap samples.

Most higher order interactions involving the factors method, season, moon phase and habitat were significant for the number of taxa caught (Table 6.3). The largest percentage of the model variation was accounted for by the method of sampling (57%). The night of sampling did not affect the number of taxa caught at any level. Overall, the plankton net caught an average of 5.8 taxa per sample, while the light trap caught only 2.4 taxa per sample. The results are complicated, however, by the significant interactions involving season, habitat and moon phase. For example, one major interaction (method x season x habitat) resulted mainly because of the larger number of taxa caught in plankton nets in the beach habitat during summer (Fig. 6.6). The fewest taxa were caught by light traps during a full moon in autumn (Fig. 6.6). Overall, more taxa were caught during summer than in autumn, but the effect of moon phase depended on all the other major factors.

Table 6.3. Analysis of variance for the total number of taxa in samples. Factors include method (plankton net and light trap), season (summer and autumn), moon phase (full and new), night (2 nights nested within season and moon phase) and habitat (reef and beach). % = percent of total variance accounted for by each factor.

Source of Variation	df	MS	F	p	%
Method	1, 4	311.76	665.09	0.000	56.9
Season	1, 4	58.59	152.03	0.000	10.7
Moon	1, 4	14.26	37.00	0.000	2.6
Night(S x Mn)	4, 70	0.39	0.76	0.558	0.3
Habitat	1, 4	12.76	94.23	0.000	2.3
Method x Season	1, 4	27.09	57.80	0.000	4.9
Method x Moon	1, 4	0.84	1.80	0.251	0.2
Season x Moon	1, 4	0.84	2.19	0.213	0.2
Method x Night(S x Mn)	4, 70	0.47	0.92	0.459	0.3
Method x Habitat	1, 4	31.51	104.31	0.000	5.8
Season x Habitat	1, 4	11.34	83.77	0.000	2.1
Moon x Habitat	1, 4	2.34	17.31	0.014	0.4
Night(S x Mn) x Habitat	4, 70	0.14	0.27	0.899	0.1
Method x Season x Moon	1, 70	2.34	5.00	0.028	0.4
Method x Season x Habitat	1, 70	33.84	112.03	0.000	6.2
Method x Moon x Habitat	1, 70	1.76	5.83	0.018	0.3
Residual	70	0.49	0.50	0.611	6.3

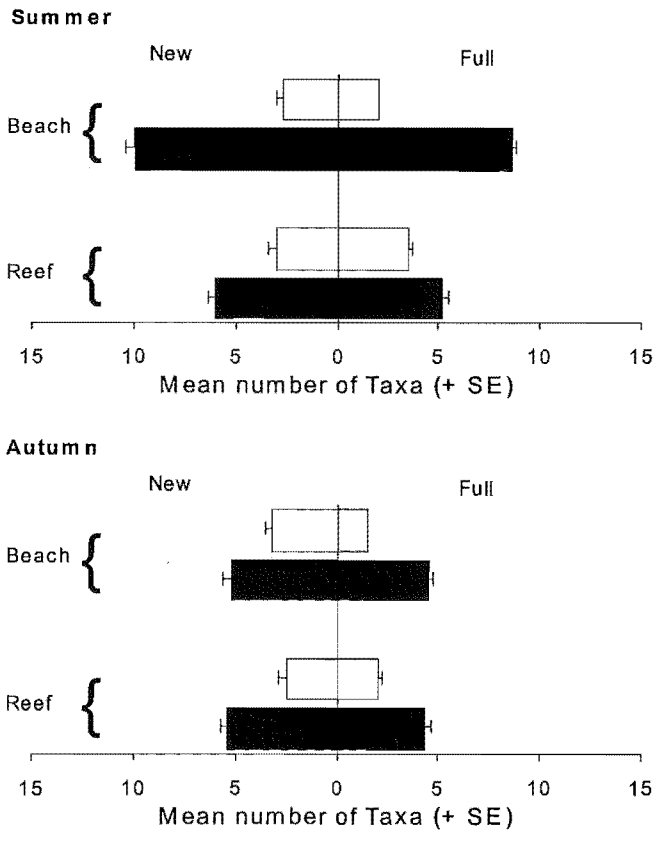

Figure 6.6. Mean number of taxa (+ SE) in samples collected in two seasons (summer and autumn) by two sampling methods (plankton net (solid bars) and light trap (open bars)) in two habitats (beach and reef) during two moon phases (new and full).

The ability to identify tripterygiid larvae to species level was closely related to the size of the larvae (Fig. 6.7). Unidentified tripterygiid larvae were significantly smaller than identified larvae (K-S test $p < 0.001$), although the 3 mm size class contained mostly the distinctive larvae of *R. decemdigitatus*. In this case, differences in the size-selectivity of each method could easily explain the discrepancy in the relative abundance of unidentified tripterygiid larvae in samples from plankton nets and light traps. To remove this bias from the comparison of the two sampling methods, unidentified tripterygiids were excluded from the Canonical Discriminant Analysis.

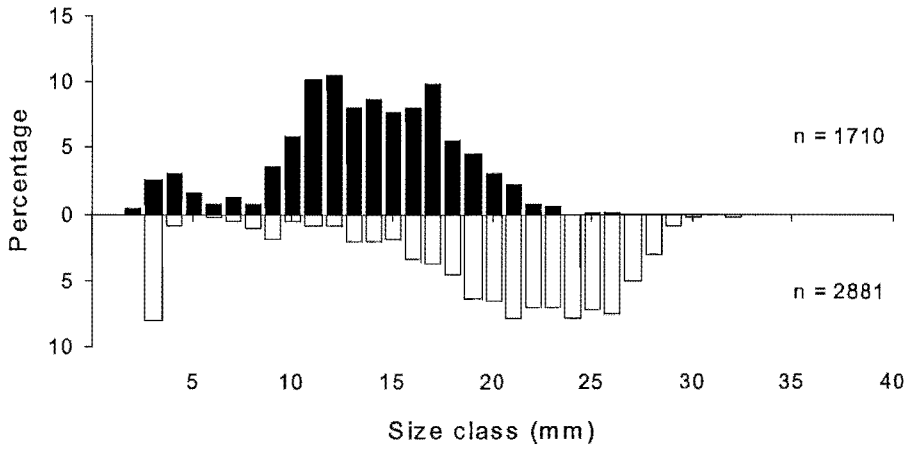

Figure 6.7. Size distribution of unidentified tripterygiid larvae (solid bars) and tripterygiid larvae identified to the species level (open bars). Data from the plankton net and light traps are combined.

Discriminant functions one and two accounted for 85% of the variation in the data set (Table 6.4). Discriminant function 1 is positively correlated with the proportion of retropinnids in the samples. Discriminant function 2 is negatively correlated with the proportion of *G. tripennis* and *R. plebeia* in the samples.

Table 6.4. Factor structure coefficients from the Canonical Discriminant Analysis of the relative proportion of each taxon taken by each sampling method within season, moon phase and habitat. Data were log (x+1) transformed. Taxon marked * are highly correlated with the discriminant function. Also shown are the eigenvalues for each discriminant function and the cumulative proportion of (common) variance extracted by each discriminant function.

Taxa	Root 1	Root 2
Sprattus spp.	-0.03	-0.20
Retropinnidae	0.93*	-0.01
Trachelochismus melobesia	-0.12	-0.08
Forsterygion lapillum	-0.07	0.04
Forsterygion varium	-0.05	-0.08
Gilloblennius tripennis	-0.06	-0.48*
Grahamina capito	-0.10	0.06
Ruanoho decemdigitatus	-0.09	-0.17
Cologrammus flavescens	-0.03	0.07
Grahamichthys radiata	-0.01	-0.26
Gobiopsis atrata	-0.04	-0.22
Rhombosolea plebeia	0.01	-0.42*
Eigenvalue	236.12	21.08
Cumulative Proportion	0.784	0.854

All samples collected in summer contained a low proportion of retropinnids (Fig. 6.8). The light traps and the plankton net each sampled a discrete fish fauna. Light trap samples were characterised by the absence of *G. tripennis* and *R. plebeia*, while the plankton net samples contained both of these taxa. Each group of replicates from the light traps was tightly clustered, indicating a high degree of consistency both within and among nights. Plankton net replicates were less tightly clustered and thus less uniform in their composition.

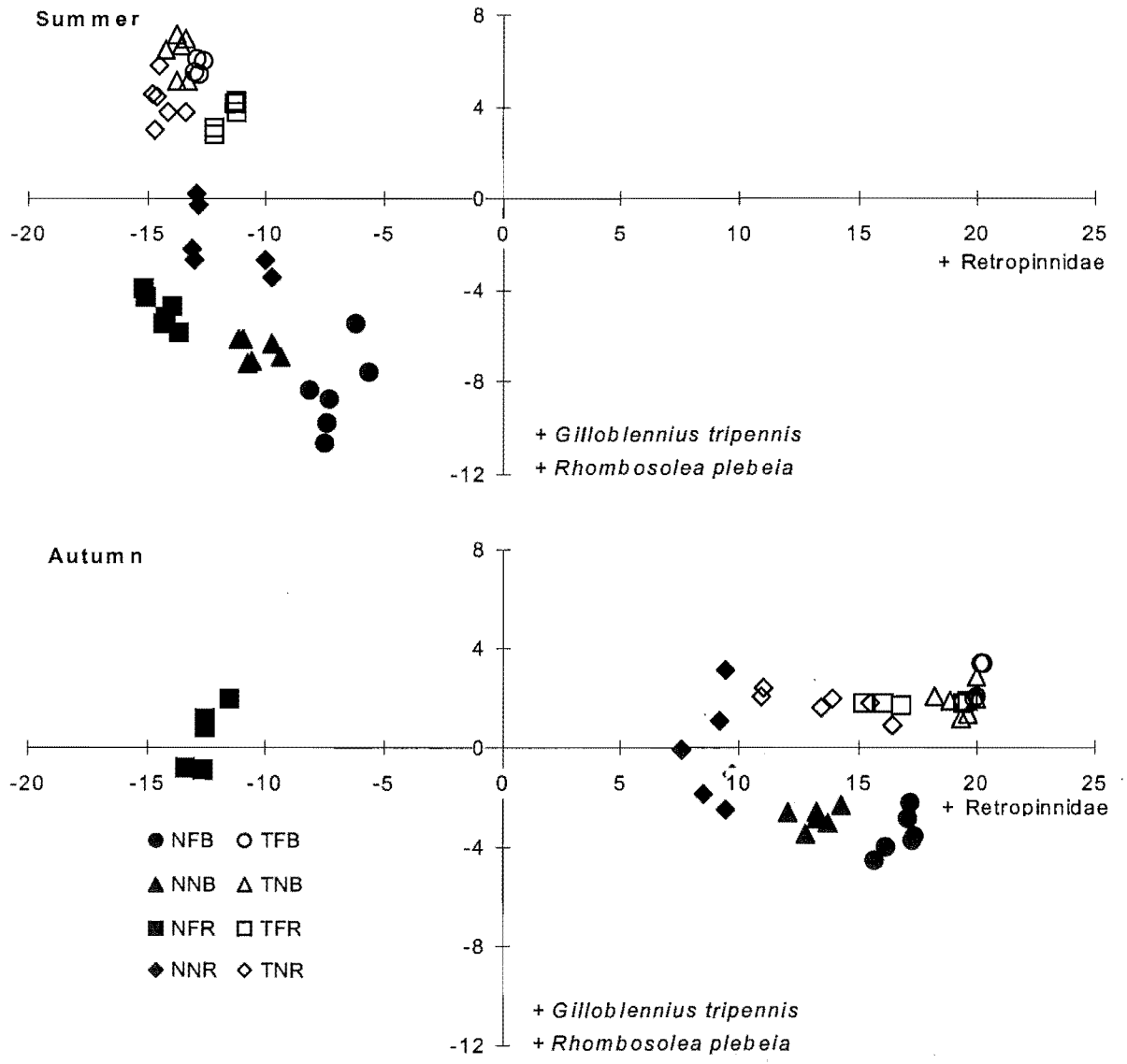

Figure 6.8. Results of Canonical Discriminant Analysis on proportional abundance of twelve taxa (for taxa used see Table 6.4) in light trap samples and standardised plankton net samples collected in summer and autumn. Canonical variates 1 and 2 are displayed. Codes for samples: (NFB) plankton net, full moon, beach habitat; (TFB) light trap, full moon, beach habitat; (NNB) plankton net, new moon, beach habitat; (TNB) light trap, new moon, beach habitat; (NFR) plankton net, full moon, reef habitat; (TFR) light trap, full moon, reef habitat; (NNR) plankton net, new moon, reef habitat; (TNR) light trap, new moon, reef habitat.

The composition of samples taken by both methods in autumn changed markedly from that seen in summer. All autumn samples (Fig. 6.8) contained a higher proportion of retropinnids than in summer. The only exceptions to this were the samples collected by the plankton net in the reef habitat during a full moon. These six replicates all contained relatively few retropinnids. The distinction between the samples collected by the plankton net and those collected by the

light traps is less clear in autumn. However, the light trap samples can still be separated on the basis that they contained no *G. tripennis* and *R. plebeia*.

In the plankton net samples, the common taxa, except for the retropinnids, were more abundant in summer than in autumn (Fig. 6.9). Retropinnids were also more abundant in the light trap samples in autumn (Fig. 6.9). Two other taxa, unidentified tripterygiids and *F. varium*, were more abundant in the autumn light trap samples than in the summer samples.

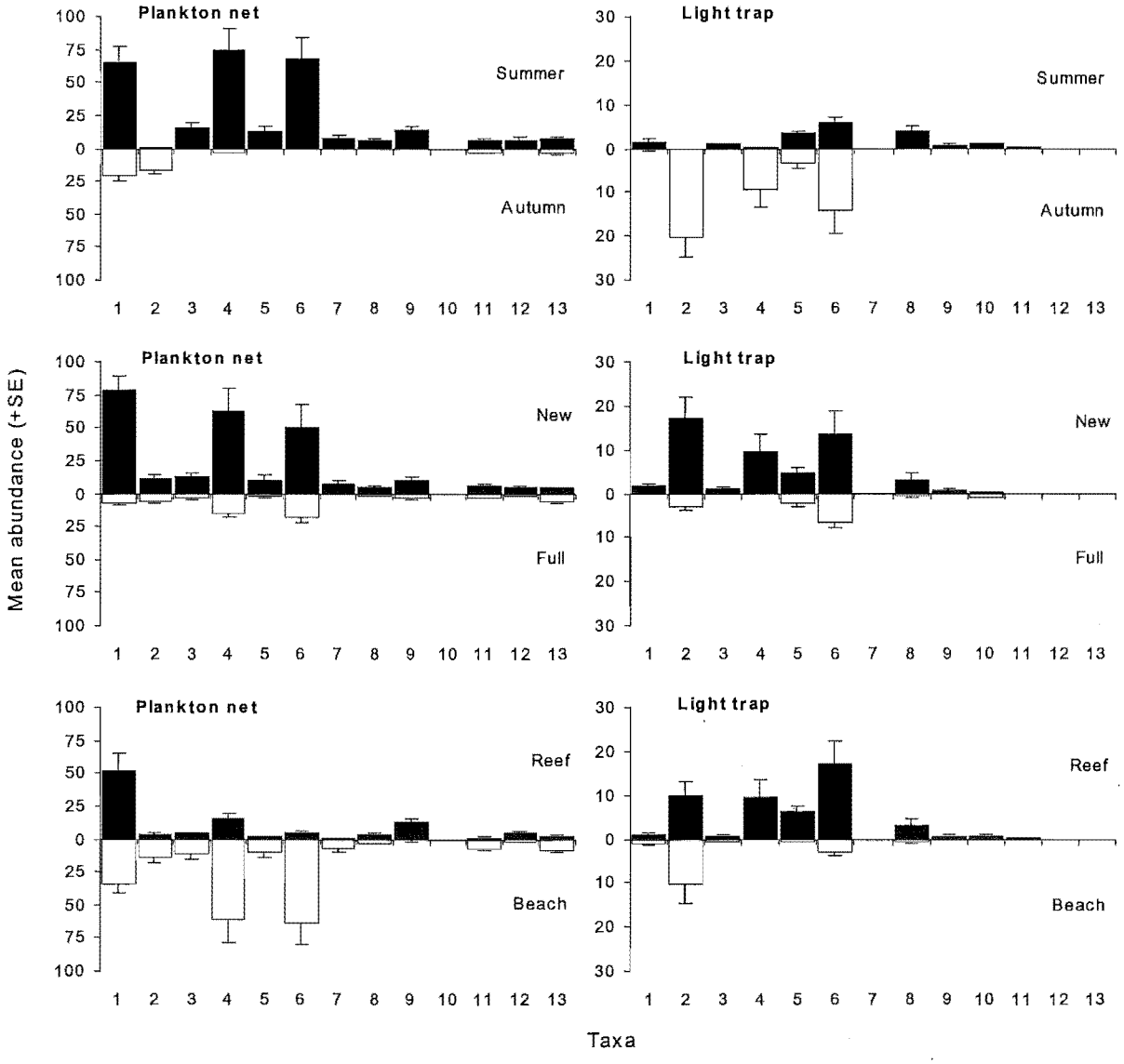

Figure 6.9. Mean abundance (+ SE) of taxa collected by the plankton net (per 200 m^3) and the light traps (per sample) during two seasons, two phases of the moon and in two habitats. Key to taxa: 1 *Sprattus* spp.; 2 retropinnids; 3 *T. melobesia*; 4 Unidentified tripterygiids; 5 *F. lapillum*; 6 *F. varium*; 7 *G. tripennis*; 8 *G. capito*; 9 *R. decemdigitatus*; 10 *C. flavescens*; 11 *G. radiata*; 12 *G. atrata*; 13 *R. plebeia*.

Most of the common taxa were more abundant in the plankton net samples during a new moon than during a full moon (Fig. 6.9). The only exception to this was *R. plebeia* which was more abundant in the full moon samples. All taxa, with the exception of *C. flavescens*, were more abundant in the new moon light trap samples than in the full moon samples (Fig. 6.9).

The light traps and plankton net indicated very different abundance patterns between habitats for most common taxa. Most taxa, except *Sprattus* spp. and *R. decemdigitatus*, were more abundant in the plankton net samples from the beach habitat (Fig. 6.9). The light traps

detected the opposite abundance patterns for most taxa. Most of the common taxa except the retropinnids were more common in the reef habitat (Fig. 6.9).

6.4 Discussion

The taxonomic composition of larval fish in the samples was clearly dependent on the sampling method. The plankton net captured more taxa than the light traps, but many of these taxa were rare in the samples. All twelve taxa taken by the light traps were present in the plankton net samples. Although the light traps sampled a subset of the taxa captured by the plankton nets, the relative abundance of individual taxa in the two methods was only weakly correlated.

Differences in the relative abundance of individual taxa between samples taken by the two methods were usually associated with differences in size-frequency distributions. The mean size of fish larvae in light trap samples was greater than that of plankton net samples for all of the common taxa. Of all the taxa, retropinnids had the most similar size distributions between methods. This is likely to be a consequence of the relatively large size of all retropinnid larvae sampled. By 20mm SL retropinnid larvae are strong swimmers (Stephens 1983) and easily capable of reaching the light trap. My results suggest that larger pelagic stages are more likely to be attracted to and swim into a light trap than are small stages, which is similar to the findings of Choat *et al.* (1993) in tropical waters. As a result of this selectivity, taxa that are only represented by small individuals in the plankton are less likely to occur in light trap samples unless they have a strong swimming ability, a strong positive phototactic response, or both.

In several cases, taxa that were abundant in the plankton net samples did not occur in the light trap samples (e.g., *G. tripennis, G. atrata* and *R. plebeia*). This could be taken as evidence of these taxa not being positively phototactic. However, most of these fish were very small and their absence from the light trap samples is likely to be a consequence of poor swimming ability. However, the light trap samples did contain very small individuals from two species of Gobiesocidae, suggesting that these species either possess a strong positive phototactic response during their early life, or are capable swimmers while still small, or a combination of both of these factors.

Samples taken by plankton nets also can be selective, both in terms of their taxonomic composition and size distribution. By actively filtering fish larvae from a water mass, plankton net characteristics, such as towing speed (Nakamura 1992), mesh size (Somerton & Kobayashi 1989), and mouth diameter (Thayer *et al.* 1983), interact with physical parameters such as light levels and water clarity (Brander & Thompson 1989), as well as the behavioural response of the fish larvae themselves (Leak & Houde 1987), to determine the composition and size structure of a sample. While small individuals may be under-represented in light trap samples, larger fish larvae are better able to avoid plankton nets (Brander & Thompson 1989) and consequently may be under-represented in plankton tows. Net avoidance is lessened at night, either through reduced visual avoidance, or reduced activity levels (Brander & Thompson 1989). Therefore, by using both methods at night, any differences in size distributions, due to net avoidance alone, should be decreased.

Little is known of the diel vertical distribution of larval fish in the study area. The vertical distribution of larval fish could affect the relative performance of the two sampling methods. It has been suggested that light traps may collect fish from the upper 5 m in tropical areas (P. J. Doherty unpublished, cited in Choat *et al.* 1993, Brogan 1994b). This collection zone is likely to be less in my study area because of suspended matter in the water. However, my light traps appeared to illuminate the water within a radius of ca. 3 m, were anchored 1 m below the surface and, therefore, were likely to have sampled fish from the upper 4 m (i.e., most of the water column at the two study sites). Conversely, the plankton net sampled a relatively narrow depth stratum, with the mouth fixed at a depth of 1 m. If any of the taxa present in the samples showed stratification in their vertical distribution, with a peak abundance outside the depth stratum sampled by the plankton net, it is likely that they would be under-represented in the samples. The extent of this bias between sampling methods is likely to vary with the depth of water at the sample site.

A major advantage of light traps over plankton nets is the ease with which light trap samples can be simultaneously replicated, by using multiple automated light traps. In deploying a plankton net, particularly in shallow rocky water with a small research boat, replicates can usually be obtained only by taking sequential tows. The time difference between replicate samples may result in increased inter-replicate variation. On most sampling occasions, replicate light trap samples were less variable than the associated plankton tows. This reduced variance will make the light traps, when used in a structured design, more sensitive to detecting differences among treatment means.

The volume of water that a light trap samples for any particular taxon is unknown (Brogan 1994b). Consequently, it is not possible to calculate accurate sample volumes and compare relative efficiencies between sampling methods. However, Choat *et al.* (1993) estimated their light traps sampled tens of thousands of m^3 per hour. Using their reasoning, an estimate can be made for the light traps used in my study. The size distributions of retropinnids caught in the two sampling methods appeared to be the most similar of all taxa collected. The two sampling methods also collected similar total numbers of this family. Using the mean number of retropinnids collected in the plankton net tows (8.88 per 200 m^3) and in the light trap samples (20.29 hour $^{-1}$), and assuming the two methods sample retropinnids with equal efficiency, then the light traps must sample ca. 450 m^3 hr^{-1}. This is considerably less than the 40,000 m^3 hr^{-1} estimated by Choat *et al.* (1993) for their study area. There are several possible reasons for this disparity. The very high mean current speed (15cm s^{-1}) given by Choat *et al.* (1993) for their study area was much greater than that encountered in my study area. This would have exposed their light traps to considerably more water. Also, the poor water clarity in my study area would have decreased the light field of light traps. These two factors combined could potentially account for the nearly 100 fold difference in sample volumes.

Both sampling methods detected seasonal differences in the samples. Most taxa had a higher abundance in the summer samples. One exception to this was the retropinnids, which occurred almost exclusively in the autumn samples. Retropinnids are anadromous, with mature fish migrating during late summer and early autumn into freshwater to spawn (McDowall 1990).

Consequently, retropinnid larvae are unlikely to appear in significant numbers in summer samples. The remaining taxa are predominately spring/early summer spawners (Ruck 1980, Ayling & Cox 1987, Paulin & Roberts 1992). The two sampling methods were generally in agreement with the patterns of seasonal abundance of individual taxa. Exceptions to this were unidentified tripterygiids, *Forsterygion lapillum* and *Forsterygion varium* that showed higher relative abundances in the autumn light trap samples. This may be a result of the size-selectivity of the light traps. During summer, tripterygiid larvae are common (as seen in the plankton net catch), but there are likely to be few large individuals for the light traps to attract. By autumn, the smaller individuals have grown to a size where they are more capable swimmers and more easily attracted to the light traps. These larger individuals may not appear in the plankton net samples because they are close to settlement and consequently are found close to the substrate. For each of the three tripterygiid taxa, the larvae caught by the light traps in autumn were larger than those caught by the plankton net in summer (K-S test $p < 0.001$). However, there was no significant difference between the sizes of larvae caught by the light traps in summer and autumn.

Both sampling methods detected lunar differences in the samples. Most taxa had a higher abundance in samples collected during a new moon. While this pattern may be the result of a real difference in abundance between lunar phases, the efficiency of both sampling methods has been linked to light intensity. Avoidance of plankton nets is greater with increased light intensity (Thayer *et al.* 1983, Brander & Thompson 1989) and the catch of light traps has been found to be negatively correlated with moon illumination (Gregory & Powles 1985). Therefore, it would be expected that both sampling methods would capture fewer fish larvae during a full moon than during a new moon regardless of the relative abundance of the larvae during the different lunar phases.

The two sampling methods detected very different patterns of abundance between the two habitats. The light traps collected more of most taxa in the reef habitat, while the plankton nets collected more in the beach habitat. An obvious reason for this discrepancy would be that smaller fish larvae were more abundant in the beach habitat and were captured by the plankton net, while larger larvae were more abundant in the reef habitat and captured by the light traps. However, further analysis of the size structure of the samples taken by the two methods did not show this pattern. There are several other possible reasons for this discrepancy. Suspended matter, disturbed by wave action at the beach site, meant that the water clarity at the beach site was worse than at the reef site. This may have reduced the radius inside which fish could detect and be attracted to the light trap. Consequently, the light trap catches would be greater in the clearer water over the rocky reef. Another possible reason for the discrepancy in patterns detected by the two sampling methods is that there may have been a difference in water current speed at the two sites. Doherty (1987) identified this factor as being of paramount importance when comparing samples taken with light traps at fixed locations. *Sprattus* spp. and retropinnid larvae, which were generally larger than other taxa and consequently stronger swimmers, may have been less affected by current speed. This could explain their relatively equal abundances in the two habitats.

My study shares four families (Clupeidae, Gobiesocidae, Tripterygiidae and Gobiidae) with Brogan (1994b), one of the two other studies comparing light traps and plankton nets. Brogan (1994b) recorded little overlap in the size distribution of clupeids caught by the two sampling methods. The two size distributions for tripterygiids broadly overlapped, but the modal size classes differed markedly. Brogan (1994b) attributed much of this variation to fish larvae avoiding daytime tows with small nets. Such avoidance, particularly by larger and therefore faster swimming fish larvae, has been demonstrated in several other studies (Clutter & Anraku 1968, Barkley 1972, Suthers & Frank 1989). Both avoidance and diel vertical migration ensure that samples taken during daylight will not be equivalent to those taken at night (Leis 1991a). In my study, both clupeid and individual tripterygiid species' size distributions overlapped broadly, but their means differed significantly. It is likely that by using both sampling methods at night the avoidance of plankton nets by larger fish was decreased.

Both previous studies comparing light traps and plankton nets in marine waters found that light traps collected fewer families than associated plankton tows. Brogan (1994b) reported that his light traps collected four families that were not present in the plankton net samples. However, these families each accounted for a very small proportion ($\leq$ 0.03%) of the total light trap catch. Neither my study nor Choat *et al.* (1993) recorded any families in light trap samples that were not present in plankton net samples.

Of the 19 large inshore species whose adults were seen in extensive surveys of reefs around the Kaikoura Peninsula (Hickford & Schiel 1995), only three (*Scorpaena papillosus*, *Aldrichetta forsteri* and *Notolabrus celidotus*) were caught as larvae by either sampling method. These taxa were not abundant in the plankton samples collected. Larvae of *Latridopsis ciliaris*, *Notolabrus fucicola* and *Odax pullus* which, together with *Notolabrus celidotus,* dominate the inshore ichthyofauna were not found in my plankton samples. The reasons for the absence of these and other common species from the plankton samples are not clear, but probably involve a narrow depth distribution or extended offshore development. It is noteworthy that Kingsford & Choat (1989) found very few larvae of common reef-dwelling fish in their plankton net samples in northern New Zealand.

In summary, the light traps used in this study attracted and captured only a subset of the taxa caught by the plankton net. The relative abundance of individual taxa in the light trap samples was very different to that in the plankton net samples. For all commonly occurring taxa, the light traps collected significantly larger fish larvae than the plankton net. The light traps were as capable as plankton nets in detecting inter-seasonal and lunar phase differences in fish larvae abundance. Water clarity and current speed should be equivalent between sites when using light traps for comparative studies. In this study, the light trap samples complemented those taken by the plankton net. While the plankton nets captured more small fish larvae and individuals from rare taxa, the light traps captured more large larvae which may have avoided the plankton net. Rather than choosing between the two methods, both can be usefully combined in a sampling programme to provide a more comprehensive insight into the ichthyoplankton spectrum associated with nearshore rocky reefs.

Chapter Seven

Distribution of Larval Fish around Surface Slicks

7.1 INTRODUCTION

In areas of mesotides (2-4 m) and narrow continental shelves (<30 km), internal waves may transport larval fish towards shore (Shanks 1983, Kingsford & Choat 1986, Pineda 1994). Internal waves are generated when a shallow thermocline or halocline is displaced by wind forcing (Phillips 1977, D'Asaro 1984), a change in current speed (Rattray 1960, Cresswell & Boland 1981) or tidal currents (Halpern 1971, Haury *et al.* 1979). The density differential across the vertically displaced thermocline or halocline leads to a gravitational restoring force (Pond & Pickard 1978) which produces internal waves.

Tidally generated internal waves occur as the tide ebbs off a continental shelf or across some topographic high (a reef or bank) on the shelf. The flow of water forms a depression in the lee of the barrier (Lee & Beardsley 1974, Gargett 1976, Haury *et al.* 1979, Maxworthy 1979). The depression causes the thermocline or halocline to be displaced vertically, which generates internal waves . When the tide floods, the internal wave packet is uncoupled from the barrier and usually propagates towards shore (Haury *et al.* 1979).

The presence of internal waves can often be detected visually by secondary effects if the layer of water above the thermocline is not very thick (Fig. 7.1). As the internal waves move, the upper layer gets thicker and thinner, producing convergences and divergences (Ewing 1950). The convergences may cause bands of irregular ripples on the sea surface above them by compressing short surface waves making them steeper and more visible, while there is smoother water over the divergences. The ripples are located just behind the crests of the internal waves (Pond & Pickard 1978). When the surface layer is thicker, the convergence in the upper layer accumulates organic material on the surface (Ewing 1950). This changes the surface tension of the water, which suppresses any ripples that would be formed by a light surface wind, and produces a surface slick. Buoyant flotsam is carried into the convergence zone by the surface currents, but because of its buoyancy it resists the downwelling currents and becomes trapped at the surface in the slick. If the internal wave and its associated convergence zone moves towards shore, it will carry the trapped flotsam with it. The proposed mechanism of larval transport by internal waves suggests that if organisms can remain near the surface in the convergence zone either through swimming or buoyancy, then they, like the flotsam, will remain in the slick (Franks 1992) and be transported onshore (Shanks 1988).

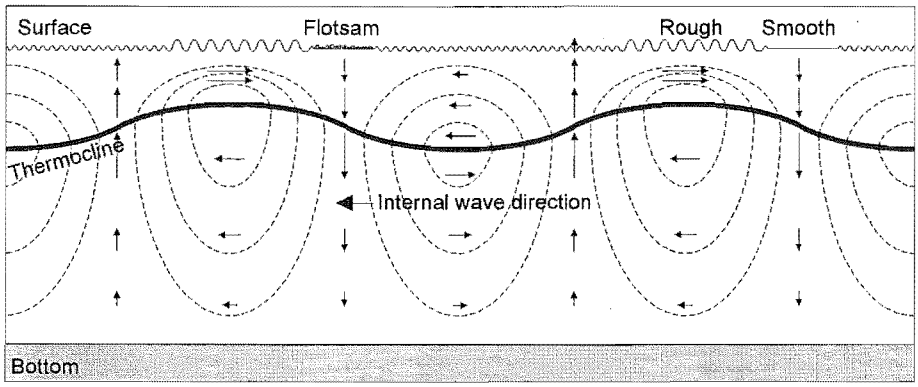

Figure 7.1. Diagram of internal wave characteristics showing zones of convergence and divergence (adapted from Ramsay (1962)).

Several authors have found evidence that planktonic larvae accumulate in the slicks of internal waves and have thus suggested that this may be a mechanism of shoreward transport. Evidence that planktonic larvae may accumulate in or be transported by the surface slicks of internal waves has been found off southern California (Shanks 1983, 1985, 1986, Pineda 1994), in the San Juan Archipelago (Shanks & Wright 1987), off North Carolina (Shanks 1988), off southeastern New Zealand (Zeldis & Jillett 1982, Jillett & Zeldis 1985) and off northeastern New Zealand (Kingsford & Choat 1986). While observations of accumulation of plankton in surface slicks dominate the knowledge of the effects of internal waves on the distribution of planktonic organisms, recent studies have found that planktonic concentrations may extend throughout the water column (Rogachev *et al.* 1996, Kushnir *et al.* 1997, Lennert-Cody & Franks 1999).

Most researchers have compared abundances of fish larvae in the surface slicks of internal waves with those in rippled areas adjacent to the slicks (Shanks 1983, 1988, Kingsford & Choat 1986, Pineda 1994). The higher abundances of fish larvae found in the slicks provided evidence of accumulation, and given the speed and direction of travel of the internal waves it was assumed that this could produce appreciable shoreward transport of larvae.

If larval fish are being accumulated by and transported in the surface slicks of internal waves, then you would expect to not only find higher densities of larvae in slicks, but that the slicks would have a sweeping effect as they passed through an area. The passage of a slick through an area should decrease the abundances of larval fish behind the slick, and increase the abundance of larvae within the slick. This prediction leads to several testable hypotheses:
1. larval fish abundances within slicks will be greater than those inshore or offshore of the slick.
2. larval fish abundances offshore from slicks will be lower than those inshore from slicks.
These hypotheses were tested by sampling offshore from, within and inshore from several solitary, shoreward moving surface slicks that were observed close to shore on the southern side of the Kaikoura Peninsula.

7.2 METHODS

7.2.1 Sampling procedure

Net Comparison - To sample effectively within slicks, a small plankton net was constructed. Prior to it being used for quantitative sampling, it was compared with a larger net to determine if it was prone to avoidance by fish larvae. This was done on the north side of the Kaikoura Peninsula during early morning on the 14th January 1997.

The large net had a 707 x 707 mm mouth (0.5 m^2) and 280 µm mesh. This net was a box-pyramid design with a mouth area : mesh area ratio of 1:11. A General Oceanics flowmeter (Model 2030R) was fitted within the mouth of the net (positioned at 0.33 of the net width) to determine the volume of water filtered per tow. The net was rigged to be towed alongside a 6 m boat to avoid disturbance caused by the wake. The top of the net frame was suspended from a gantry so that it sampled at a fixed depth. A 25 kg Scripps depressor was suspended from the lower edge of the frame to keep the net mouth vertical in the water column. The upper edge of the mouth of the net was held at 0.5 m below the surface of the water. The net was towed with

a four-point bridle that joined above the level of the mouth of the net to avoid disturbance caused by the wire strops.

The smaller net had a 250 x 250 mm mouth (0.0625 m^2) and 280 µm mesh. It was also a box-pyramid design, but with a filtration efficiency of 1:14. A General Oceanics flowmeter (Model 2030R) was fitted within the mouth of the net (positioned at 0.33 of the net width) to determine the volume of water filtered per tow. The top of the net frame was attached to a pole that could be lowered beside the boat so that the uppermost edge of the net was fixed at a depth of 0.5 m.

Three replicates were collected by each of the plankton nets in alternating order. Each net was towed for 5 min at a speed of ca. 1.2 ms^{-1}. The large net filtered an average of 148 m^3 of water per replicate. The smaller net filtered an average of 35 m^3 per replicate.

Sampling around slicks - The location of slicks determined where the comparative sampling was done. However, the three slicks that were sampled each occurred between Baxter's Reef and Atia Point extending across the entrance of South Bay (Fig. 7.2). Winds were very light at the time (early morning) that slicks were observed. The slicks were evident as an accumulation of large amounts of floating material (foam, driftwood and seaweed) in a single ribbon which was ca. 3 m wide and in all cases over 500 m long. The slicks were aligned parallel to the coast.

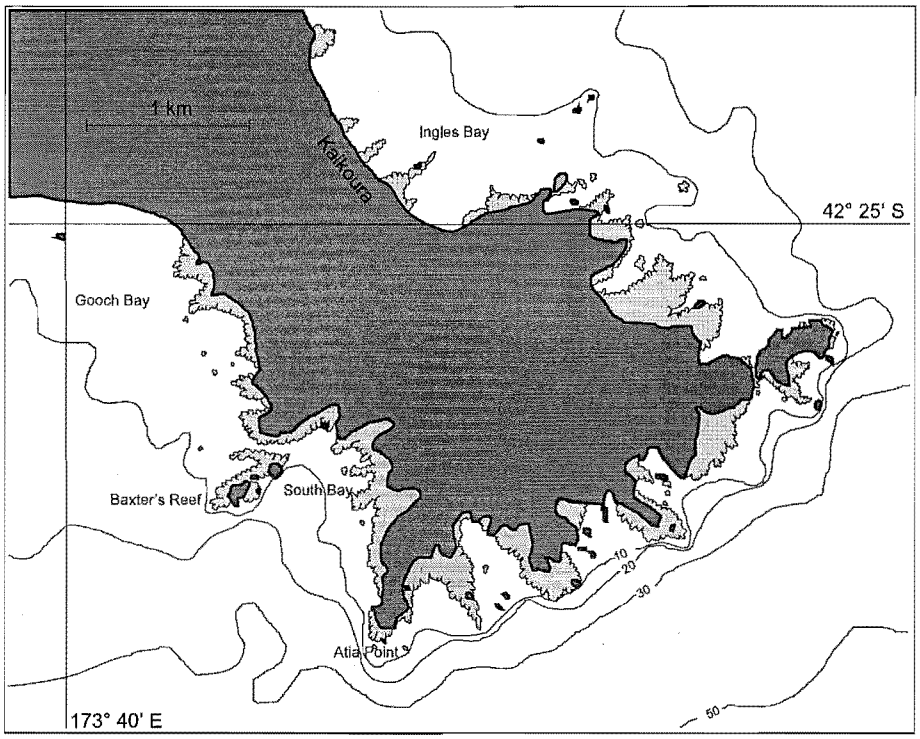

Figure 7.2. Map of the Kaikoura Peninsula on the northeast coast of the South Island. Bathymetry in metres.

The small plankton net was used to sample ichthyoplankton at a depth of 0.5 m in the vicinity of the slick. Three replicate samples were taken within the slick, 50 m offshore from the slick and 50 m inshore from the slick. The samples were collected parallel to the slick and taken in random order. The position of a recognisable object within the slick (usually a piece of driftwood) was recorded using a Trimble Ensign GPS (accurate to ± 10 m) prior to each of the three samples within the slick, to determine if the slick as a whole was moving.

After the completion of each sample, the plankton net was washed thoroughly with pumped seawater and the sample was fixed in buffered 10 % formalin in seawater. All fish larvae were removed from the samples using a dissection microscope, identified to the lowest possible taxonomic level, counted and stored in buffered 2 % formalin in freshwater. Counts were standardised to the number of fish per 50 m^3. Clupeid and retropinnid larvae could not be identified beyond the family or genus level because of the similarities of larvae from individual species and the presence of adults from several species of each of these families in the study area. Small scorpaenids and tripterygiids could also not be identified below the family or genus level. All fish (except those that were badly damaged) were measured to the nearest 0.5 mm by placing them on a graduated slide. Notochord length was measured for preflexion and flexion larvae, and standard length was measured for postflexion larvae.

7.2.2 Analysis

Two types of data were collected during this study. The ichthyoplankton samples contained a wide range of taxa, allowing tests on the abundance of individual taxa and species richness. Because all undamaged fish larvae were measured, the size of larvae could also be compared between samples.

Net Comparison - Counts of fish larvae in the samples were standardised to the number of fish per 50 m^3. A two factor ANOVA, with plankton net (2 sizes) and taxa (9 taxa) as factors, was used to compare the abundance of all taxa in the samples collected by the two plankton nets. Prior to ANOVA, the data were tested for homogeneity of variances using Cochran's test, and all data became homogeneous when log (x+1) transformed. Tukey Honest Significant Difference (HSD) tests were used for *post hoc* comparison of means.

A one-way ANOVA was used to compare the size of larvae collected by the two plankton nets. Prior to ANOVA, the data were tested for homogeneity of variances using Cochran's test.

Sampling around slicks - Counts of fish larvae in the samples were standardised to the number of fish per 50 m^3. Two factor ANOVAs were used to compare taxonomic richness and the abundance of common taxa on three occasions (treated as random) and in three areas (offshore from, within and inshore from the slick). Prior to ANOVA, the data were tested for homogeneity of variances using Cochran's test, and all but taxonomic richness required log (x+1) transformation to become homogeneous. Tukey HSD tests were used for *post hoc* comparison of means.

One-way ANOVAs were used to compare the size of common taxa found in the three areas (occasions were combined). Prior to ANOVA, the data were tested for homogeneity of variances using Cochran's test.

7.3 RESULTS

Net Comparison - The taxonomic composition of the samples collected by the two plankton nets broadly overlapped, but several of the taxa that were rare in the large net were not found in the samples taken with the smaller net (Fig. 7.3). However, *G. tripennis* and *G. capito* were the only taxa that showed a significant difference in mean abundance between the two nets

(Tukey HSD, $p < 0.05$). Most of the variability in the data set was due to differences in the abundance of individual taxa (Table 7.1).

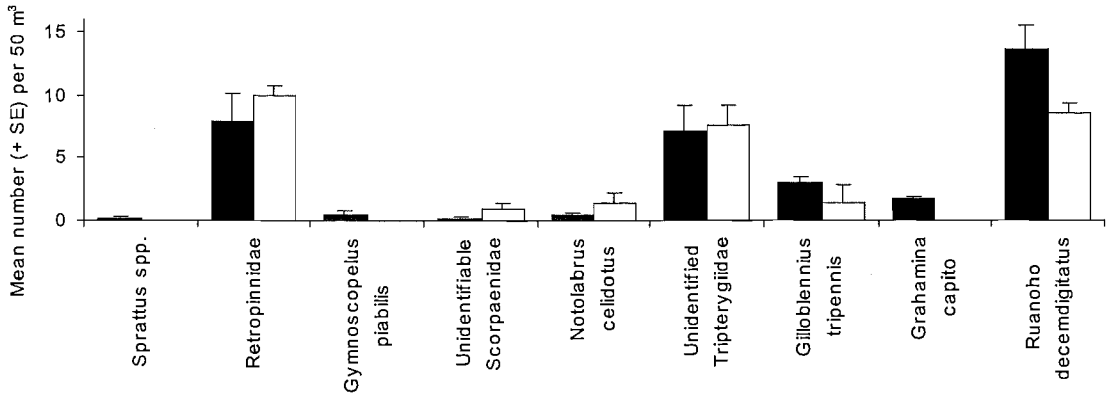

Figure 7.3. Mean abundance (+ SE) per 50 m^3 of nine taxa caught at 0.5 m depth in a plankton net with a 0.5 m^2 mouth (solid bars) and a smaller plankton net with a 0.0625 m^2 mouth (open bars).

Table 7.1. Results from ANOVA of the abundance of fish larvae per 50 m^3, with plankton net (2 sizes) and taxa (9 individual taxa) as factors. The variance has been partitioned (%) for each factor and the interaction term.

Factor	df	MS	F	p	%
Net	1	0.07	2.29	0.139	0.7
Taxa	8	1.03	35.33	0.000	83.0
Net x Taxa	8	0.07	2.46	0.031	5.8
Residual	36	0.03			10.6

The few *G. tripennis* that were collected by the 0.0625 m^2 plankton net were smaller on average than those in the larger net (Table 7.2). For the three other common taxa, there was no difference in the mean size of larvae collected by the two nets. The largest larva caught by the small net was a 16 mm retropinnid, and by the larger net was a 31.5 mm *Sprattus* spp..

Table 7.2. Results from ANOVA of the sizes of larvae from the four most common taxa collected by a large (0.5 m^2) and small (0.0625 m^2) plankton net. The number of larvae measured (n) and their mean size (mm) is given for each net.

Taxon	ANOVA result	0.5 m^2		0.0625 m^2	
		n	Mean (mm)	n	Mean (mm)
Retropinnidae	$F_{1,85} = 0.02$, $p = 0.88$	66	12.1	21	12.0
Unidentified Tripterygiidae	$F_{1,79} = 0.67$, $p = 0.42$	65	8.9	16	9.4
G. tripennis	$F_{1,17} = 7.15$, $p < 0.05$	26	7.7	3	3.7
R. decemdigitatus	$F_{1,134} = 0.39$, $p = 0.53$	118	7.3	18	7.7

Sampling around slicks - Each of the slicks sampled was moving in a NW direction (towards shore) at an average speed of 0.21 ms^{-1} (0.76 kph) (Table 7.3). The accumulation of flotsam in the slicks appeared stable throughout the sampling period. However, on one occasion the wind

increased in strength noticeably during sampling and, as a result of a surface chop, the slick became difficult to differentiate in some areas.

Table 7.3. Summary of the movement patterns of the three slicks including direction travelled, distance travelled and speed.

Date	Direction (°)	Distance (m)	Time (min)	Speed (m s^{-1})
16th January 1997	345	135 ± 20	15	0.15 ± 0.02
17th January 1997	286	265 ± 20	15	0.29 ± 0.02
7th February 1997	313	159 ± 20	15	0.18 ± 0.02

Overall, more taxa were found within slicks than offshore or inshore from them (Table 7.4). However, two taxa (*H. abdominalis* and *C. kumu*) were found inshore from slicks, but not within the slicks. On each occasion, the mean taxonomic richness within a slick was greater than that either side of it (Fig. 7.4). However, there was too much variability between replicates for this difference to be significant (Table 7.5). The taxonomic richness of the samples varied markedly between occasions.

Table 7.4. Composition and size range of fish larvae in the samples. Total abundance (n), percentage of total catch when adjusted for volume (%), mean size ($\bar{x}$), minimum size(-) and maximum size (+) (mm) of larvae found offshore from, within and inshore from a slick are given for each taxon.

Family	Taxon	Offshore					Within					Inshore				
		n	%	$\bar{x}$	-	+	n	%	$\bar{x}$	-	+	n	%	$\bar{x}$	-	+
Clupeidae	*Sprattus* spp.	1	1.8	14.5	14.5	14.5	1	0.3	10	10	10	2	1.2	13.5	11	16
Retropinnidae	Retropinnidae	2	3.7	9	7.5	10.5	12	3.6	21.8	13.5	25.5	4	2.7	15.6	14	18
Gobiesocidae	*Diplocrepis puniceus*	4	7.6	3	3	3	3	1.0	3.2	3	3.5	1	0.6	5.5	5.5	5.5
Syngnathidae	*Hippocampus abdominalis*											1	0.6	16.5	16.5	16.5
Scorpaenidae	Unidentifiable Scorpaenidae	8	15.3	1.9	1.5	3	19	5.8	1.9	1.5	3	5	3.8	1.7	1.5	2
Triglidae	*Chelidonichthys kumu*											1	0.7	14.5	14.5	14.5
Acanthoclinidae	*Acanthoclinus fuscus*	1	1.8	6	6	6	1	0.3	6	6	6	1	0.6	5	5	5
Mugiligae	*Aldrichetta forsteri*						1	0.3	3.5	3.5	3.5					
Tripterygiidae	Unidentified Tripterygiidae	5	9.4	10.7	5.5	12.5	28	8.4	9.7	2	16	19	13.4	9.4	4	14
	Forsterygion spp.	13	25.8	8.0	6.5	11	40	12.2	6.8	4	11	25	16.5	6.2	4.5	9
	Forsterygion lapillum						1	0.3	9	9	9					
	Forsterygion varium	1	2.1	11	11	11	12	3.6	12.6	9	17.5	6	4.2	15.1	13	16.5
	Gilloblennius tripennis	7	14.4	6.1	3.5	7.5	4	1.3	5.9	4.5	7	6	4.0	7.4	6	9.5
	Grahamina capito	1	1.9	9.5	9.5	9.5	4	1.2	11.6	11	12.5					
	Ruanoho decemdigitatus	7	14.1	4.2	3	5.5	195	60.6	3.5	3	5.5	78	50.4	3.7	3	4.5
Monacanthidae	*Parika scaber*						2	0.6	15.5	13.5	17.5	1	0.6	18.5	18.5	18.5
	Damaged	1	2.1				1	0.32				1	0.6			
Total		51	100	6.3	1.5	14.5	324	100	5.6	1.5	25.5	151	100	5.9	1.5	18.5

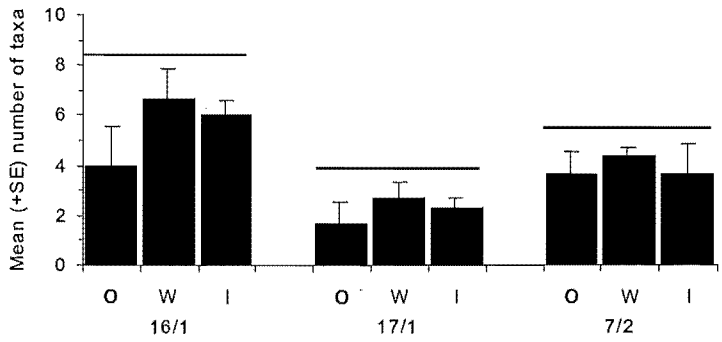

Figure 7.4. The mean taxonomic richness (+SE) of samples taken offshore from (O), within (W) and inshore from (I) a slick on three occasions (16th,17th January and 7th February 1997). Areas that are under a horizontal line on the same plane are not significantly different (Tukey HSD, $p > 0.05$).

The abundance of larvae from all taxa differed consistently between areas on each occasion (Table 7.5). Significantly more larvae were found within the slicks than offshore from the slicks (Fig. 7.5). However, there was no significant difference between the total number of larvae within the slicks and those inshore of the slicks. On all three occasions, there was no significant difference between the number of larvae offshore and inshore from the slick. The mean size of larvae from all taxa combined did not differ significantly between the three areas ($F_{2,506} = 0.84$, $p = 0.43$) when the three occasions were combined (Fig. 7.6).

Table 7.5. Summary results from ANOVA of the taxonomic richness and abundance of five taxa, with occasion (3 slicks) and area (offshore, within and inshore) as factors.

Taxon	Occasion		Area		Interaction	
	$F_{2,18}$	p	$F_{2,4}$	p	$F_{2,18}$	p
Taxonomic richness	9.64	**	4.30	ns	0.43	ns
All taxa	13.33	**	24.02	**	1.10	ns
Unidentified Scorpaenidae	7.79	**	1.18	ns	1.59	ns
Unidentified Tripterygiidae	76.32	***	1.31	ns	6.07	**
Forsterygion spp.	57.92	***	2.03	ns	0.93	ns
Ruanoho decemdigitatus	80.92	***	2.68	ns	15.51	***

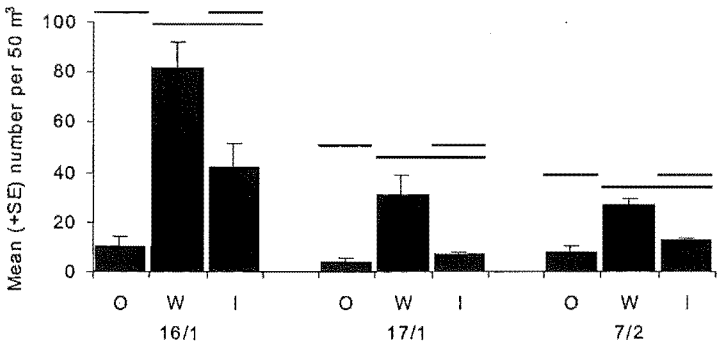

Figure 7.5. The mean abundance (+SE) of larvae from all taxa found offshore from (O), within (W) and inshore from (I) a slick on three occasions (16th,17th January and 7th February 1997). Areas that are under a horizontal line on the same plane are not significantly different (Tukey HSD, $p > 0.05$).

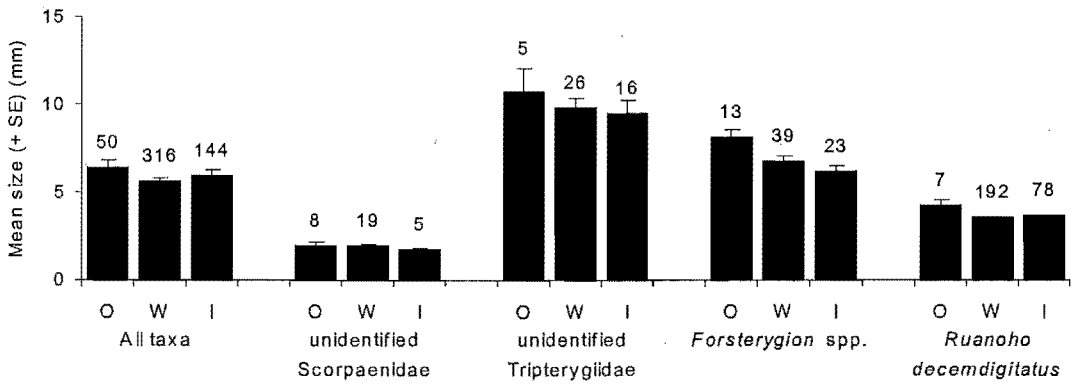

Figure 7.6. Mean size (+SE) (mm) of all taxa and the four most common taxa found at 0.5 m depth offshore from (O), within (W) and inshore from (I) a slick on three occasions. The number of larvae measured is given above each bar.

The abundance of unidentified scorpaenid larvae differed between occasions, but not consistently between areas (Table 7.5). On the first two occasions, there was no significant difference between the areas in the abundance of unidentified scorpaenids (Fig. 7.7). On the last occasion, significantly more larvae were found within the slick. The mean size of scorpaenid larvae did not differ significantly between the three areas ($F_{2,29} = 0.56$, $p = 0.579$) when the three occasions were combined (Fig. 7.6).

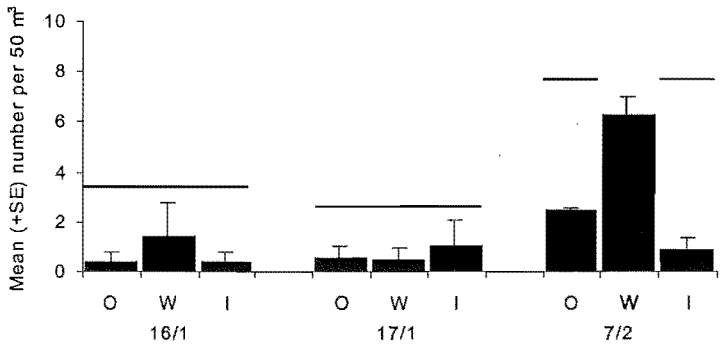

Figure 7.7. The mean abundance (+SE) of unidentified scorpaenid larvae found offshore from (O), within (W) and inshore from (I) a slick on three occasions (16th,17th January and 7th February 1997). Areas that are under a horizontal line on the same plane are not significantly different (Tukey HSD, $p > 0.05$).

The abundance of unidentified tripterygiid larvae differed between occasions, but not consistently between areas (Table 7.5). On the first two occasions, abundances were very low (Fig. 7.8). However, on the last occasion, significantly less tripterygiid larvae were found offshore than within the slick. The mean size of tripterygiid larvae did not differ significantly between the three areas ($F_{2,44} = 0.29$, $p = 0.745$) when the three occasions were combined (Fig. 7.6).

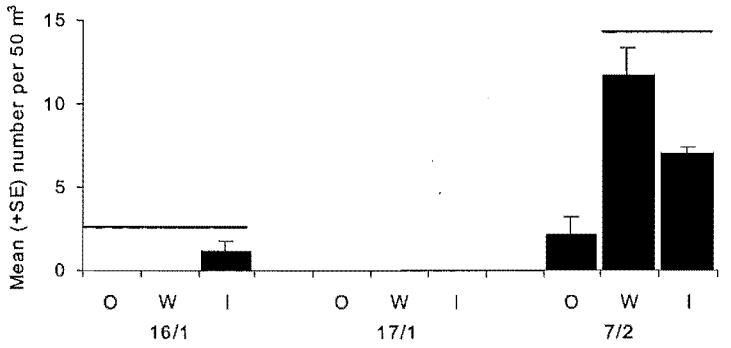

Figure 7.8. The mean abundance (+SE) of unidentified tripterygiid larvae found offshore from (O), within (W) and inshore from (I) a slick on three occasions (16th,17th January and 7th February 1997). Areas that are under a horizontal line on the same plane are not significantly different (Tukey HSD, $p > 0.05$).

The abundance of *Forsterygion* spp. larvae differed between occasions, but not consistently between areas (Table 7.5). On the first occasion, significantly more *Forsterygion* spp. larvae were found within the slick than offshore (Fig. 7.9). On the other two occasions, the abundance of *Forsterygion* spp. larvae did not differ significantly between areas. Larvae found offshore from the slick were significantly larger ($F_{2,72} = 5.89$, $p < 0.01$) than those found within or inshore of the slick (Fig. 7.6).

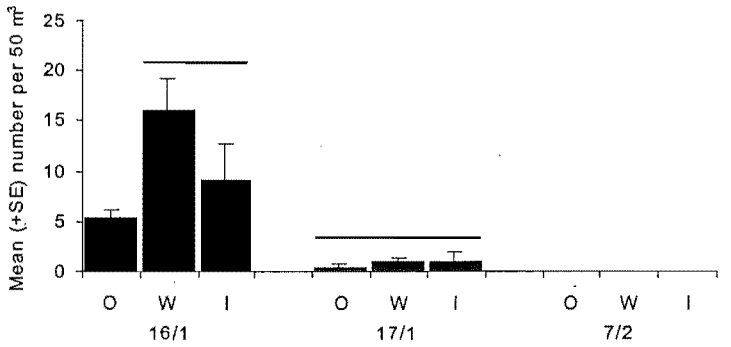

Figure 7.9. The mean abundance (+SE) of *Forsterygion* spp. larvae found offshore from (O), within (W) and inshore from (I) a slick on three occasions (16th,17th January and 7th February 1997). Areas that are under a horizontal line on the same plane are not significantly different (Tukey HSD, $p > 0.05$).

The abundance of *R. decemdigitatus* larvae differed between occasions, but not consistently between areas (Table 7.5). On the first two occasions, significantly more *R. decemdigitatus* larvae were found within the slick than offshore (or inshore on the second occasion) (Fig. 7.10). Very few *R. decemdigitatus* larvae were found on the last occasion. Larvae found offshore from the slick were significantly larger ($F_{2,274} = 15.50$, $p < 0.001$) than those found within or inshore of the slick (Fig. 7.6).

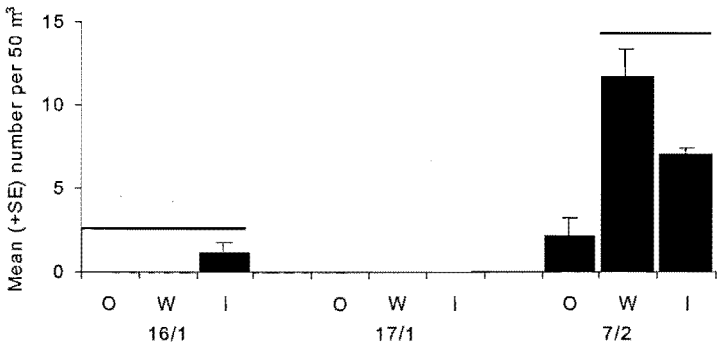

Figure 7.10. The mean abundance (+SE) of *Ruanoho decemdigitatus* larvae found offshore from (O), within (W) and inshore from (I) a slick on three occasions (16th,17th January and 7th February 1997). Areas that are under a horizontal line on the same plane are not significantly different (Tukey HSD, $p > 0.05$).

7.4 DISCUSSION

Net comparison - The composition of the samples taken by the two plankton nets was very similar when adjusted for volume. However, several taxa that were rare in the samples taken with the larger net were not collected by the small net, and some taxa that were represented mainly by large individuals were less abundant in the small net. The absence of rarer taxa is likely to be a result of the lower volumes of water sampled by the smaller net. Although it appears that the small net may suffer from avoidance by large individuals of some taxa (particularly *G. tripennis*), this is not true of all taxa. The smaller net collected many larvae (particularly retropinnids) that were relatively large (>12 mm).

Although the smaller volumes sampled by the smaller net may underestimate the taxonomic richness in an area and the abundance of some larger larvae, it does offer many advantages over the larger net for sampling surface slicks. The principal advantage is its increased manoeuvrability due to both its size and the way that it is towed. This manoeuvrability is very useful when sampling narrow (< 3 m wide) surface slicks. For this reason, the smaller net was used for sampling within and around surface slicks.

Sampling around slicks - The exact cause of the surface slicks observed on the south side of the Kaikoura Peninsula cannot be known without more knowledge of its physical oceanography. However, given the mesotides, narrow continental shelf and near-shore submarine canyon in the area, tidally generated internal waves are likely to be formed (Apel *et al.* 1975, Shanks 1988). The observed slicks could be the surface manifestations of these internal waves, or they may instead be the result of a tidally induced front (Kingsford *et al.* 1991). While the exact cause of the surface slicks is unknown, they were observed to move consistently towards shore at an average speed of 0.2 ms^{-1}.

Many authors have documented aggregations of planktonic organisms in shoreward moving surface slicks (Zeldis & Jillett 1982, Shanks 1983, 1985, 1986, 1988, Jillett & Zeldis 1985, Kingsford & Choat 1986, Shanks & Wright 1987, Kingsford *et al.* 1991, Pineda 1994), and inferred that these slicks may facilitate the onshore transport of planktonic larvae. However, if shoreward moving surface slicks really are transporting planktonic larvae then you would expect

to see lower abundances of larvae offshore from the slick than within the slick or inshore from it. Shanks (1988) sought to test this hypothesis, and observed abundances which suggested that the slicks were transporting planktonic larvae shoreward. However, because only a single set of internal waves was sampled, he could not rule out cross-shelf patchiness as the explanation behind the observed patterns.

In my study, the passage of a slick through an area did not appear to decrease the total abundance of larvae in the area. On each occasion, the total abundance of larvae offshore from a slick was not significantly different to that inshore from the slick. However, the abundance of larvae within the slick was considerably greater than that in the surrounding waters.

Although total larval abundance did not change with the passing of a slick, the abundance of several individual taxa did. When unidentified tripterygiid, *Forsterygion* spp. and *R. decemdigitatus* larvae were abundant, significantly fewer larvae were found offshore from the shoreward moving slick than inshore from it. For these taxa, the slick appears to be capable of concentrating larvae and transporting them towards shore.

Shanks (1988) reported that the shoreward transport of fish larvae by the surface slicks of internal waves might be confined to postflexion stage larvae. However, in my study entrainment by slicks did not appear to be size-dependent. There was no clear pattern among the common taxa in the size of larvae offshore from, within or inshore from the slick. However, the larger larvae that Shanks (1988) found within slicks may have avoided the small plankton net used in my study.

Shanks (1988) also found several species exclusively in the slicks of internal waves. These species may have been very rare outside of the slick and only seen in the slick due to its concentrating effect, or they may have been carried into the area from a distant source. There was little evidence from my study of slicks transporting larvae from a distant source into the study area. All but two taxa (*A. forsteri* and *F. lapillum*) that were found within the slicks were also present outside of the slicks. On each occasion, there was no significant difference among the taxonomic richness of samples taken offshore from, within or inshore from the slicks. However, the presence of the rarer taxa that Shanks (1988) found within slicks may have been missed by the small plankton net used in my study.

The effects of surface slicks on the larval fish entrained within them may be multi-faceted. The slicks may facilitate the onshore transport of presettlement larvae. However, the convergence zones associated with internal waves not only concentrate fish larvae, but other plankton (Shanks 1983, Kingsford & Choat 1986). The slicks may present larval fish with above-average concentrations of food necessary for survival. However, planktonic (Hamner & Schneider 1986) and avian (Haney 1987) predators are also advected into or attracted to slicks. This could lead to considerably higher predation rates within the slicks than in adjacent water. Thus, although a larval fish that spends a period of time within a slick may be transported closer to shore amongst a plentiful food source, it is also likely to experience above average predation rates.

In conclusion, while further investigation is necessary, fish larvae from several taxa are definitely concentrated within the shoreward moving slicks and have lower abundances offshore from them. For at least some taxa, therefore, the slicks may facilitate onshore transport. If a shoreward moving surface slick entrains reef fish larvae, this may be a mechanism to return these larvae to a habitat that is suitable for settlement.

Chapter Eight

Summary and General Discussion

8.1 INTRODUCTION

The central objective of this thesis was to investigate the distribution and abundance of larval fish in the pelagic environment. A set of mensurative experiments was used to describe temporal and spatial distribution patterns on broad and fine scales. The combined results of these experiments provide considerable information on the processes that are important in structuring the distribution and abundance of larval fish populations in the Kaikoura region.

8.2 DISTRIBUTION AND ABUNDANCE OF LARVAL FISH

8.2.1 Temporal distribution

The total abundance, species composition and species richness of larval fish assemblages in the Kaikoura region varied throughout the course of a year. The spawning activity of local adult populations is probably the major determinant of this broad-scale temporal variation in abundance. The timing of spawning activity appeared to be related to phytoplankton and zooplankton production cycles, as it has been in many other studies (Townsend 1984, Jenkins 1986, Haldorson *et al.* 1993, Horstman & Fives 1994). The reproductive strategy of most fish species appeared to involve synchronising peaks in larval abundance with peaks in prey abundance (Cushing 1975). This is likely to improve the survival rates of larval fish by maximising food availability. However, the larval stages of some species were pre-emptive or ubiquitous, with larvae occurring prior to peaks in zooplankton production or during periods of low prey abundance.

The timing of peaks in larval abundance was relatively constant between years for most species. However, the amplitude of these annual peaks varied considerably for some species. If this annual variability in peak abundance is indicative of fluctuations in year-class strength then the resulting recruitment variability will impact on the structure of adult populations (Sale *et al.* 1985, Doherty & Williams 1988, Doherty 1991, Sale 1991). Any annual variability in larval supply is likely to have long-lasting effects on the dynamics of local adult populations (Underwood & Denley 1984).

Despite many fine-scale differences in occurrence and peaks of abundance, there were close similarities between the Kaikoura region and northeastern New Zealand (see review by Kingsford 1988) in the temporal distribution of the larval stages of most shared species. The geographic separation and very different current and exposure regimes of the two locations did not result in marked differences in temporal distribution, with most shared taxa (especially the tripterygiids) having a broad overlap in temporal distribution between north and south. Only one species, *Aldrichetta forsteri*, showed an obvious displacement in timing. This may be the result of delayed spawning or a longer egg phase in southern populations of *A. forsteri*.

The abundance of larval fish at offshore stations often changed abruptly between fortnightly samples. Although high mortality rates could explain decreases in abundance at a station, horizontal movement is most likely responsible for this temporal variation because abrupt increases also occured. However, this horizontal movement must occur on a temporal scale finer than two weeks for intermediate states not to be detected by fortnightly sampling.

Descriptions of offshore distribution on a finer temporal scale are required to elucidate patterns of horizontal movement.

The abundance of larvae in surface waters (i.e., the uppermost 3 m) at inshore sites was relatively consistent between consecutive days. There was little change in the abundance or composition of larval assemblages at fixed sites when they were sampled at the same time of the day over short periods (3 days). This suggests that the processes producing temporal variation in abundance operate on a broader time scale. However, at inshore sites there were large variations in the abundance of larval fish in surface waters within a 24 hr period, probably because of diel vertical migration. The extent and nature of diel vertical migration require further investigation on a broader spatial scale, but also on a finer temporal scale, so that more precise patterns of nocturnal movement of larval fish, their prey and predators can be detected. Experiments that manipulate the densities of larval fish, prey species and predators in mesocosms may provide insight into the complex biological and physical relationships that generate and influence vertical migration.

8.2.2 Spatial distribution

The abundance, species composition and species richness of larval fish assemblages vary with distance off the Kaikoura coast. The abundance of the larval stages of most species was not uniform over the narrow continental shelf at Kaikoura. The larval stages of some species were consistently more abundant further from shore. These included deep water species (*Gymnoscopelus piabilis*), amphidromous freshwater species (galaxiids) and intertidal/reef species (*Bovichtus variegatus* and most tripterygiids). The larval stages of other species were always found in highest abundance near land. These included diadromous freshwater species (retropinnids), demersal species (scorpaenids and *Rhombosolea plebeia*) and inshore pelagic species (*Aldrichetta forsteri*).

In the Kaikoura region, the combination of a northward flowing coastal current (Chiswell 1996) and onshore winds produces wind-derived surface water transport towards the north-west, and thus onshore, during all seasons (Heath 1972b). However, the presence, at up to 6 km from the coast, of larvae of adult fish that spawn nearshore suggests a mechanism of offshore transport must exist. A cross-shelf recirculation cell (cf. Smith *et al.* 1999) may be one mechanism of offshore dispersal. This cell could act by transporting larvae in subsurface waters offshore and those in surface waters towards shore. To determine if such a cell exists, studies of nearshore hydrodynamics are required.

Although the abundance of larval stages of most species varied with distance from shore, there is little evidence from my study to support the generalisation that larvae that are more abundant nearshore hatch from demersal eggs, whereas those that are more widely distributed are derived from pelagic eggs (Leis & Miller 1976, Marliave 1986, Kingsford & Choat 1989, Suthers & Frank 1991, Brogan 1994a, Gray 1998). For example, the larval stages of most of the common tripterygiid species in the neuston were more abundant further from shore. These species all produce demersal eggs (Crossland 1981) and the family as a whole has been reported as having a nearshore distribution (Leis & Miller 1976, Leis 1982, Gray 1993),

particularly in the vicinity of reefs (Leis & Goldman 1984, Kingsford & Choat 1989, Brogan 1994a). The species-specific distribution patterns observed for tripterygiids suggest that it is simplistic to attempt to characterise the offshore distribution of a family as a whole.

The observed nearshore distributions of the larval stages of many species that hatch from demersal eggs has been attributed to the absence of passive drift during the egg phase and their generally larger size (Thresher 1984) which may give them the superior swimming and sensory abilities (Blaxter 1986, Miller *et al.* 1988) necessary to maintain a nearshore distribution (Suthers & Frank 1991). Although some species that hatch as relatively large larvae from demersal eggs (retropinnids) did maintain a nearshore distribution in my study, other species with very similar spawning strategies were more abundant further from shore (galaxiids). The contrasting spatial distributions of these families is considered to be the result of differing dispersal requirements necessitated by differing longevity and adult migration patterns (McDowall 1996).

Although the larval stages of many species were dispersed at least 6 km off the Kaikoura coast, the larval stages of some species, including several that were abundant offshore, appeared to resist alongshore dispersal. Coastal currents provide a clear mechanism for the dispersal of neustonic larvae along the coast in the Kaikoura region (Chiswell & Schiel In Review). Species with restricted alongshore distribution may use a combination of active swimming (Leis 1982), schooling behaviour (Kingsford 1986, Marliave 1986, Breitburg 1989) or eddies to prevent alongshore dispersal. However, the larval stages of species that are dispersed offshore and returned to the nearshore environment by cross-shelf advection may utilise alongshore currents to transport them to suitable settlement habitats.

Acting within the broader-scale distribution patterns of larval fish were fine-scale processes. These processes are usually undetected by broad scale surveys, but may contribute to the often considerable variation observed in large scale studies (Fasham 1978, Haury *et al.* 1978, Fortier & Leggett 1984, Leis 1991a, Williams & English 1992, Lennert-Cody & Franks 1999). Both the horizontal and vertical distribution of larval fish in my study were influenced by processes operating on a fine scale.

The horizontal distribution of larval fish in inshore surface waters is strongly influenced by the presence of surface slicks. The exact causes of these slicks, in the Kaikoura region, is unknown, but they are likely to be surface manifestations of internal waves. Abundances of fish larvae were considerably higher within surface slicks than in surface waters either side of them. This aggregation, together with the shoreward movement of slicks, suggests that they may transport larval fish towards shore. The decreased abundance of larval fish in an area after the passage of a surface slicks shows they are capable of modifying broad-scale distribution patterns. Although the scale of interest when studying surface slicks was metres, the aggregation and movement of internal waves may influence spatial variability on a much broader scale.

The vertical distribution, beyond 3 m depth, of larval fish in the coastal waters around the Kaikoura Peninsula is undescribed. However, larval fish in the uppermost 3 m of water had a fine-scale vertically stratified distribution in my study. This vertical distribution varied between

individual species and changed within a 24 hr period. The distribution and abundance of zooplankton in the uppermost 3 m of the water column also changed within a 24 hr period. Diel vertical migration of larval fish and zooplankton was considered to be the major process producing variation in the fine-scale vertical distribution patterns. Vertical migration in larval fish is influenced by biological and physical stratification of the water column (see review by Neilson & Perry 1988). Any distributional change in either the food source or predators of larval fish is likely to influence their vertical distribution. For some species, the degree of vertical migration by larvae appeared to be affected by ambient light levels. These light levels may act directly on the vertical migration behaviour of larval fish or indirectly by modifying the vertical distribution of their predators or prey.

8.3 METHODS OF SAMPLING LARVAL FISH

With processes acting on a range of scales and in several dimensions, it is clear that no single method is appropriate for all ichthyoplankton sampling. This study relied predominately on horizontal plankton tows at the surface and at fixed depths for sampling the larval stages of fish. While fixed depth tows do not provide a detailed picture of fish larvae in the whole water column, the alternative method of stepped oblique tows may hugely underestimate larvae in discrete depth bands. This is particularly true of the neuston, which is usually rich with larval fish (Hempel & Weikert 1972, Andres & John 1984), but poorly sampled by oblique tows (Smith & Richardson 1977). A variety of other filtering and aggregation methods are available to sample different components of the ichthyoplankton, but the usefulness of each method is related to environmental conditions or habitat type.

Light traps are a useful passive device for sampling larval fishes in marine habitats, but they have been rarely used in temperate areas. Light traps attracted and captured larval fish in inshore habitats around the Kaikoura Peninsula. Although the light traps caught a subset of the species taken by plankton nets, they were equally capable of detecting seasonal and lunar phase differences in larval fish abundance. Light traps offer many advantages over plankton nets for sampling in shallow inshore waters. Multiple automated light traps can be used to take replicates simultaneously. This reduces inter-replicate variation and makes the light traps, when used in a structured design, more sensitive to detecting differences between treatment means. The passive nature of light traps makes them selective in the size and species of larval fish that they collect, but it also means they are able to be used in very shallow water. Because light traps are capable of collecting large numbers of settlement-stage fish (Doherty 1987, Milicich *et al.* 1992, Milicich & Doherty 1994), they will be very useful for establishing links between larval supply and recruitment on rocky reefs.

8.4 PROCESSES OF RECRUITMENT

My study found large numbers of larval fish, whose adults inhabit the nearshore environment, in surface waters up to 6 km from the coast. This dispersal and the processes that influence the broad-scale transportation of larval fish may play a key role in determining spatial and temporal recruitment variability. Although offshore dispersal may be beneficial during the

pelagic phase of fish (Johannes 1978, Barlow 1981, Doherty *et al.* 1985), it also necessitates onshore transportation prior to settlement. The constancy of these transportation mechanisms will determine the level of recruitment variability.

The predominant current in the Kaikoura region is the Southland current, which flows northwards parallel to the coast (Chiswell 1996). This current is clearly a mechanism for dispersal of pelagic larvae along the coast, but it is transportation perpendicular to this flow that is likely to influence recruitment rates. Two mechanisms that are capable of producing such perpendicular movement, by over-riding the broad scale current patterns, are onshore winds and internal waves.

"The main wind-derived water transport at Kaikoura is onshore during all seasons" (Heath 1972b). This transport is likely to be the result of Langmuir circulations. These are commonly observed as parallel streaks (windrows) formed when the wind blows across the surface of the water. The streaks are a series of counter-rotating vortices aligned approximately parallel to the direction of the wind. The streaks observed at the surface correspond to the convergence of two vortices. Larval fish in surface waters are aggregated by these convergences. Coupled to the vortices is a perturbation in the downwind water velocity. The downwind velocities are higher in the convergence zones than in the divergence zones. Thus, the movement of accumulated particles, including larval fish, in these circulations will be downwind. If the winds are onshore, as is predominately the case on the Kaikoura coast (Heath 1972b), then the movement of larval fish will also be onshore.

Larval fish are also accumulated in and transported by the slicks of internal waves (Shanks 1983, 1988, Kingsford & Choat 1986). Unlike windrows, the direction of movement in the slicks of internal waves is perpendicular to the slick. Surface slicks in the Kaikoura region were observed to move shoreward at velocities averaging 0.2 ms^{-1}. These slicks are likely to be the surface manifestations of tidally generated internal waves. The regular generation and shoreward movement of internal waves and their surface slicks may be a mechanism of onshore transport for larval fish in surface waters.

The persistent adult populations of inshore species along the Kaikoura coast suggest that the combined actions of onshore transport mechanisms must be sufficient to return dispersed larvae of these inshore species to the coast prior to the end of their pelagic phase. However, variability in the occurrence and effectiveness of these mechanisms is likely to be important in structuring adult populations by producing a variable larval supply.

8.5 CONCLUSION

The information gathered in this study confirms the observation that the larval stages of fish are not passive particles at the mercy of local currents (Leis & Goldman 1984). Although local oceanographic processes can directly influence the broad-scale distribution of larval fish, these distributions can be modified markedly by fine-scale processes and the behaviour of larval fish. The ability of the larval stages of many species of fish to adjust their horizontal and vertical position and to maintain a station in suitable habitats results in distributions that are both structured and complex.

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Appendix 1

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Evaluation of the performance of light traps for sampling fish larvae in inshore temperate waters

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ABSTRACT: We compared 2 methods of collecting fish larvae in inshore temperate waters near the Kaikoura Peninsula, New Zealand: night collection with light traps and with a plankton net. The sampling design incorporated seasons (summer and autumn), moon phases (full and new) and habitats (reef and beach). The 2 methods were simultaneously deployed over 2 nights in replicates of 3 within each factor. The resulting 96 samples captured 8086 larvae from 14 families. The plankton net captured twice as many taxa from twice as many families as the light traps. No taxa were caught exclusively by the light traps. For all taxa, the fish larvae collected by the light traps were larger than those in the plankton net samples. Most taxa were more abundant in the summer and new moon samples taken by both methods. The 2 methods indicated different abundance patterns between habitats for most taxa. The light traps collected more of most taxa in the reef habitat, while the plankton net collected more in the beach habitat. The light trap samples complemented those taken by the plankton net. Both sampling methods could be combined in a sampling procedure to provide a more comprehensive picture of inshore ichthyoplankton assemblages.

KEY WORDS: Fish larvae · Light traps · Rocky reef · Sampling methods · New Zealand

INTRODUCTION

Because the successful completion of the pelagic phase of marine teleost fishes is crucial to subsequent fish populations, there has been considerable research on ichthyoplankton and the processes influencing survival and settlement of fish larvae from the open water community. A large portion of this work involves sampling and development of appropriate techniques to determine species composition and size classes of the ichthyoplankton in different environments. Although methods and equipment for sampling ichthyoplankton in open water are well developed, usually involving towing multiple plankton nets from large research vessels, most are not practicable for sampling in shallow inshore waters, particularly near rocky reefs. Many methods have been used for sampling ichthyoplankton close to reefs, including diver-guided plankton nets (Brogan 1994), moored nets (Kingsford & Finn 1997), purse seines (Kingsford & Choat 1985), plankton pumps (Powlik et al. 1991), visual censuses (Kingsford & Choat 1989), aggregation devices that attract fish into collection sites (Victor 1991) and light traps (Doherty 1987). However, it is clear that different methods usually sample different components of the ichthyoplankton, and the usefulness of each method is related to environmental conditions or types of habitat.

Light traps are useful passive devices for sampling larval fishes in marine habitats and have been instrumental in understanding larval abundance patterns along the Great Barrier Reef (Milicich & Doherty 1994, Thorrold & Williams 1996). However, only 2 studies, both done in the tropics, have compared the performance of light traps with plankton nets, which are extensively used for sampling ichthyoplankton in marine waters. Light traps have rarely been used in temperate areas, and it is not known how useful they are in sampling the larval fish community in these less diverse regions. For example, the cold, murky waters of southern New Zealand support only ca 70 species of coastal fishes while the Great Barrier Reef supports more than 1500 fish species. Both the lower diversity

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and poorer water clarity of temperate waters are likely to affect the sampling properties of light traps and may limit their usefulness in these areas.

Light traps exploit the positive phototactic response of larval and juvenile fishes. Therefore, their success depends on the ability of larvae to see a light, to swim towards it and enter an illuminated enclosure (Brogan 1994), all of which may change during ontogeny (Bulkowski & Meade 1983) or with light intensity and wavelength (Gehrke 1994). It is generally accepted that light traps are both species- and size-selective (Gregory & Powles 1985, 1988, Doherty 1987, Thorrold 1992, 1993, Choat et al. 1993, Brogan 1994) and, therefore, it is necessary to determine the sampling properties of light traps before incorporating them into a sampling design.

The purpose of our study was to compare light traps and plankton nets for sampling the inshore larval fish community. Our general question was whether these 2 methods yielded the same taxonomic composition, relative abundance of taxa and size-frequency of fish larvae. Because the ichthyoplankton can vary seasonally, with the phase of the moon and by habitat, we incorporated these as factors in our sampling design. We, therefore, posed as null hypotheses that the light trap and plankton net samples would be identical in 2 inshore habitats, 2 seasons and 2 moon phases.

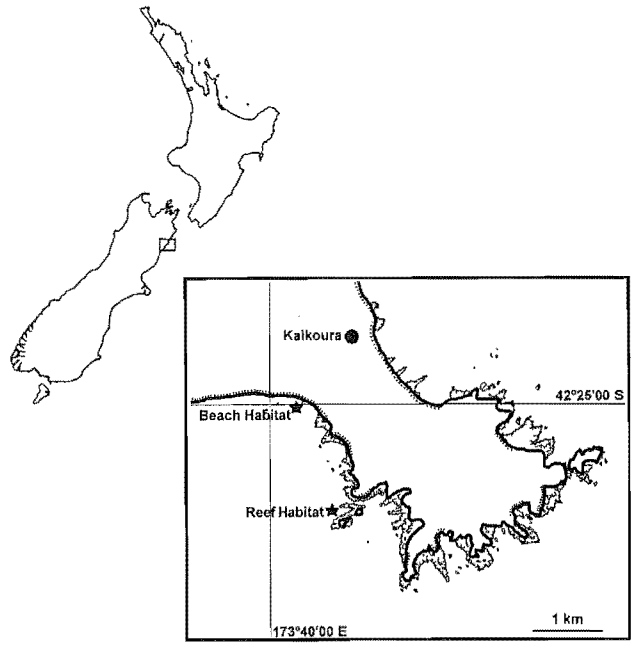

Fig. 1. Kaikoura Peninsula, New Zealand, showing position of beach and reef habitat sampling sites

METHODS

Study area. Sampling was done at 2 sites on the southern side of the Kaikoura Peninsula, on the east coast of the South Island, New Zealand (Fig. 1). The first site (reef habitat) had a rocky reef substrate with dense beds of macroalgae (predominately *Marginariella boryana* and *Carpophyllum maschalocarpum*) and a mean depth of 4.2 m. It was interspersed with deep channels (maximum depth 9 m) and rocky pinnacles. The second site (beach habitat) was adjacent to a fine shingle beach (5 to 10 mm particle diameter), was free of macroalgae and was situated over a gently sloping sandy substrate. It had a mean depth of 4.5 m and a maximum depth of 8 m. The nearest rocky reef was ca 300 m alongshore. The 2 sites were separated by rocky promontories and a distance of 1.6 km.

Sampling gear. We constructed light traps that were a modified version of those described by Doherty (1987). The body of the light trap (Fig. 2) was made from a 240 l mobile plastic waste bin (Sulo, Australia), divided by 2 opaque partitions into 3 chambers. Three sides of the upper chamber were fitted with clear plastic windows (290 × 190 mm), each containing 2 moulded entrance slots. Each horizontal slot tapered from 60 × 300 mm down to 12 × 250 mm. The partitions separating the chambers contained 2 identical slots. The middle chamber had no external entrance slots but was fitted with a 250 × 300 mm clear plastic window. The lower chamber was fitted with 0.5 mm stainless steel mesh panels (240 × 150 mm) on 3 sides and a 50 mm drain hole (closed with a rubber stopper).

A central waterproof core ran through all 3 chambers. The upper section of the core was constructed from 150 mm wastepipe and contained a rechargeable lead-acid battery (12 V, 10 Ah) and a digital timing mechanism. The lower section of the core was constructed of 40 mm clear plastic tube and contained the 3 light sources (6 W fluorescent tubes). Each of the light sources was contained solely within a chamber. The timer mechanism was identical to that described by Doherty (1987), with the light in the lower chamber remaining lit throughout the sampling sequence and the lights in the upper and middle chambers alternating at 5 min intervals.

The plankton net had a 707 × 707 mm mouth (0.5 m^2) and was constructed from 280 µm mesh. The net was a box-pyramid design with a filtration efficiency of 1:12. A General Oceanics digital flowmeter (Model 2030R) was fitted in the mouth of the net (at 0.33 of the net width) to determine the volume of water filtered per tow. The net was towed with a 4-point bridle alongside a 6 m boat. The net was rigged so that it sampled with the uppermost edge of the mouth of the net at a fixed depth of 1 m and was towed for 5 min at a speed of ca 1 m s^{-1}.

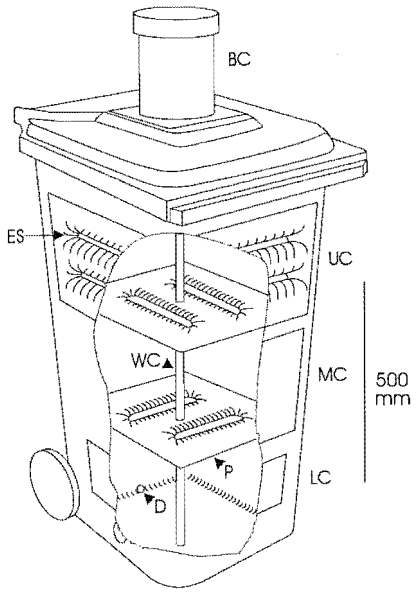

Fig. 2. Diagram of a light trap with the side partially cut away (BC: battery chamber; UC: upper chamber; MC: middle chamber; LC: lower chamber; P: partition; D: drain; WC: waterproof core; ES: entrance slot)

Sampling procedure. The reef and beach habitats were sampled on 2 nights during both a new moon (30 January 1997 and 3 February 1997) and a full moon (17 February 1997 and 21 March 1997) in summer. This sampling design was repeated during a new moon (31 March 1997 and 2 April 1997) and a full moon (15 April 1997 and 17 April 1997) in autumn. On each night, the 2 different sampling methods were deployed in both habitats. The 2 habitats were sampled in random order using the following method: 2 h after dusk, 3 automated light traps were deployed. Each light trap was suspended below an anchored buoy so that the entrance slots into the light trap were 1.5 m below the surface. The light traps were positioned ca 15 m apart. The 3 light traps were programmed to start simultaneously, sample for 30 min and then shut down. The light traps were left in the water for no more than 1 h in total. While the light traps were sampling, 3 replicate tows were made nearby with the plankton net. All tows were completed approximately 100 m from the anchored light traps and filtered 138 to 218 m^3 of water per tow.

After the completion of each sample, the plankton net and light traps were washed thoroughly with pumped seawater and the sample was fixed in buffered 10% formalin in seawater. All fish larvae were removed from the samples using a dissection microscope, identified to the lowest possible taxonomic level, and stored in buffered 2% formalin in freshwater. All fish (except those that were badly damaged) were measured to the nearest 0.5 mm by placing them on a graduated slide. Notochord length was measured for preflexion and flexion larvae, and standard length was measured for postflexion larvae.

For light traps, abundance is given as the number of fish per sample. Plankton net samples were standardised to the number of fish per 200 m^3.

Analysis. Two types of data were collected. Both the plankton net and light traps collected a wide range of species allowing tests of species richness between sampling procedures. Because all undamaged fish larvae were measured, sizes could be compared for fish captured by the 2 sampling methods across seasons, phases of the moon and habitat. Abundances of fish, comparing the 2 sampling methods and their interactions with other factors, could not be tested because the volume of water sampled by light traps for each species is unknown. However, a correlation coefficient was calculated for the abundance of each taxon in the samples from the 2 methods by summing the abundance of individual taxa across the 3 replicates on each sampling occasion and correlating this total with the total obtained from the other sampling method.

The size-frequency distributions of fish larvae caught by the plankton net and light traps were compared using the Kolmogorov-Smirnov (K-S) test. We tested the total fish sample and 7 individual taxa, which were selected on the basis of comprising at least 1% of the total catch in either sampling method.

To test the number of taxa caught between light traps and the plankton net across seasons, phases of the moon and habitat, a mixed model ANOVA was used with the factors method (light trap and plankton net), season (summer and autumn), moon phase (full and new), nights within season × moon phase (treated as random) and habitat (reef and beach). Prior to ANOVA, the data were tested for homogeneity of variances using Cochran's test. Post hoc pooling was used to eliminate non-significant ($p > 0.25$) higher order interactions from the model (Underwood 1997).

RESULTS

In total, the 96 samples captured 8086 larval and pelagic juvenile fish from 14 families. There was a marked difference in the taxonomic composition of the samples taken by the 2 methods. The plankton net took almost twice as many taxa from twice as many families as the light traps (Table 1) and collected a wider size-range of individuals from most taxa. Overall, the light traps caught far fewer fish larvae than the plankton net (Table 1). However, all light trap and plankton net samples contained fish larvae.

Table 1. Composition and size range of samples taken by plankton net and light trap. Data are pooled across season, moon phase and habitat. Summary of occurrences (Occ.), minimum (Min.), maximum (Max.) and mean ($\bar{x}$) size (mm standard length), total number of individuals (n) within each taxon and percentage (%) of total catch from 48 light trap samples and 48 plankton net samples

Family	Taxa	Plankton net						Light traps					
		Occ.	Min.	Max.	$\bar{x}$	n	%	Occ.	Min.	Max.	$\bar{x}$	n	%
Clupeidae	*Sprattus* spp.	47	4.0	44.0	22.3	1663	25.60	14	17.0	67.5	34.5	45	2.83
Retropinnidae	Unidentified Retropinnidae	28	13.0	61.0	34.6	359	5.53	24	20.5	62.5	35.8	487	30.65
Moridae	*Auchenoceros punctatus*	1	19.5	19.5	19.5	1	0.02	0					
Gobiesocidae	*Diplocrepis puniceus*	16	3.0	5.5	4.9	48	0.74	6	6.0	15.5	12.4	11	0.69
	Trachelochismus melobesia	28	3.0	15.5	6.3	308	4.74	18	3.5	15.5	9.6	28	1.76
	Trachelochismus pinnulatus	5	4.5	5.5	5.0	5	0.08	0					
	Paratrachichthys trailli	5	11.0	16.0	14.1	12	0.18	4	16.0	16.5	16.2	6	0.38
Scorpaenidae	Unidentified Scorpaenidae	1	2.5	2.5	2.5	1	0.02	0					
	Scorpaena papillosus	5	18.0	22.0	20.3	8	0.12	0					
Acanthoclinidae	*Acanthoclinus fuscus*	4	3.5	11.0	6.5	4	0.06	0					
Mugilidae	*Aldrichetta forsteri*	2	31.0	32.0	31.5	2	0.03	0					
Labridae	*Notolabrus celidotus*	3	10.0	14.5	12.1	4	0.06	0					
Tripterygiidae	Unidentified Tripterygiidae	42	2.0	22.0	12.9	1481	22.80	9	11.5	26.0	18.6	229	14.41
	Forsterygion lapillum	25	14.0	32.5	22.5	241	3.71	27	9.5	29.0	24.5	162	10.20
	Forsterygion varium	34	11.5	39.0	22.0	1317	20.27	32	15.0	33.5	23.5	483	30.40
	Gilloblennius tripennis	15	3.0	17.5	8.7	155	2.39	0					
	Grahamina capito	21	8.5	21.5	14.4	110	1.69	12	7.0	22.5	15.3	93	5.85
	Ruanoho decemdigitatus	22	3.0	26.0	4.5	257	3.96	7	19.5	22.0	20.4	19	1.20
Clinidae	*Cologrammus flavescens*	13	18.5	28.5	21.3	19	0.29	12	18.0	22.0	20.4	23	1.45
Eleotridae	*Grahamichthys radiata*	36	4.5	41.5	18.5	173	2.66	3	17.0	19.0	18.2	3	0.19
Gobiidae	*Gobiopsis atrata*	16	2.5	17.0	3.3	120	1.85	0					
Pleuronectidae	*Peltorhamphus* spp.	2	12.0	13.5	12.5	3	0.05	0					
	Rhombosolea plebeia	37	4.5	9.0	6.7	206	3.17	0					
Total			2.0	61.0	17.8	6497			3.5	67.5	17.9	1589	

Eleven taxa occurred exclusively in the plankton net samples (Table 1), but no taxa were caught solely by the light traps. Eight of these 11 taxa were rare, each comprising ≤0.12% of the total plankton net catch. However, the remaining 3 taxa (*Gilloblennius tripennis*, *Gobiopsis atrata* and *Rhombosolea plebeia*) were relatively common in the plankton net samples, each occurring in at least 15 of the samples and having more than 100 larvae in total (Table 1).

There was little correlation between the abundance of each taxon in the plankton net and light trap samples. Only 6 (*Sprattus* spp., unidentified Retropinnidae, *Trachelochismus melobesia*, *Paratrachichthys trailli*, *Grahamina capito*, *Ruanoho decemdigitatus*) of the 23 taxa collected showed a positive correlation ($p < 0.05$) between the abundance of fish larvae in the plankton net and light trap samples. The remainder showed little correlation or were not collected by the light trap.

In both sampling methods, a few abundant taxa dominated the catch (Table 1). The 3 most abundant taxa collected by the plankton net and light traps accounted for 68.7 and 75.4% of the catch, respectively. The abundance distribution of the plankton net samples was more balanced than that of the light traps. However, the rank of the taxa was very different between sampling methods. For example, *Sprattus* spp. was the most common taxon in the plankton net samples (25.6%), but only the 6th most common in the light trap samples (2.8%). Unidentified Retropinnidae was the most common group in the light trap samples (30.7%), but only the 4th most common in the plankton net samples (5.5%).

There were significant differences between the mean standard length of fish captured by the 2 sampling methods in all taxa tested (Fig. 3). For all taxa, larvae collected by the light traps were significantly larger than those in the plankton net samples. The few *Sprattus* spp. captured by the light traps were on average 12 mm larger than those in the plankton net samples. The larger *Sprattus* spp. larvae caught by the light traps were missing from the samples taken by the plankton net (Fig. 3). The size-frequency distributions of retropinnids caught in the light traps and plankton net overlapped broadly, but there was a slight difference in the modal size class (Fig. 3). Only 5 of the retropinnids caught were <20 mm standard length (SL), and the majority of fish larvae in samples collected by both methods were >30 mm SL. When the

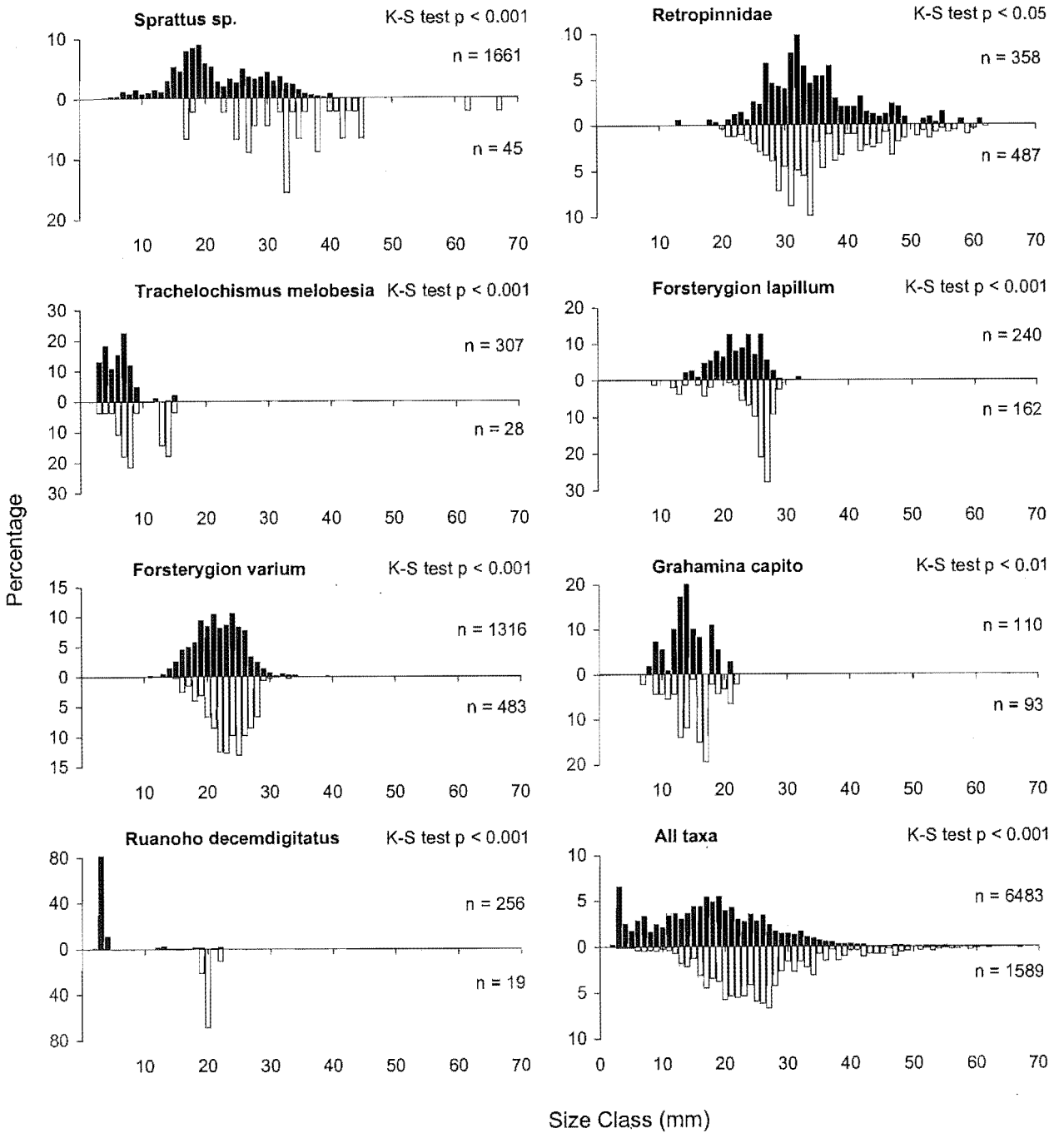

Fig. 3. Size distributions of fish larvae in plankton net samples (solid bars) and in light trap samples (open bars)

size-frequency of the total catch from the light traps is compared to that from the plankton net, it is clear that smaller individuals are more common in the plankton net (Fig. 3). Fish larvae >40 mm, which were relatively common in the light trap samples, were very rare in the plankton net samples.

The 3 taxa, *Gilloblennius tripennis*, *Gobiopsis atrata* and *Rhombosolea plebeia*, that were relatively common in the plankton net samples but absent from the light trap samples had very few individuals in the larger size classes (>10 mm) which comprised the majority of the light trap samples.

Most higher order interactions involving the factors method, season, moon phase and habitat were significant for the number of taxa caught (Table 2). The largest percentage of the model variation was ac-

Table 2. ANOVA for total number of taxa in samples. Factors include method (plankton net and light trap), season (summer and autumn), moon phase (full and new), night (2 nights nested within season and moon phase) and habitat (reef and beach) (% = percent of total variance accounted for by each factor)

Source of variation	df	MS	*F*	p	%
Method	1, 4	311.76	665.09	0.000	56.9
Season	1, 4	58.59	152.03	0.000	10.7
Moon	1, 4	14.26	37.00	0.000	2.6
Night (S × Mn)	4, 70	0.39	0.76	0.558	0.3
Habitat	1, 4	12.76	94.23	0.000	2.3
Method × Season	1, 4	27.09	57.80	0.000	4.9
Method × Moon	1, 4	0.84	1.80	0.251	0.2
Season × Moon	1, 4	0.84	2.19	0.213	0.2
Method × Night (S × Mn)	4, 70	0.47	0.92	0.459	0.3
Method × Habitat	1, 4	31.51	104.31	0.000	5.8
Season × Habitat	1, 4	11.34	83.77	0.000	2.1
Moon × Habitat	1, 4	2.34	17.31	0.014	0.4
Night (S × Mn) × Habitat	4, 70	0.14	0.27	0.899	0.1
Method × Season × Moon	1, 70	2.34	5.00	0.028	0.4
Method × Season × Habitat	1, 70	33.84	112.03	0.000	6.2
Method × Moon × Habitat	1, 70	1.76	5.83	0.018	0.3
Residual	70	0.49	0.50	0.611	6.3

counted for by the method of sampling (57%). The night of sampling did not affect the number of taxa caught at any level. Overall, the plankton net caught an average of 5.8 taxa per sample while the light trap caught only 2.4 taxa per sample. The results are complicated, however, by the significant interactions involving season, habitat and moon phase. One major interaction (method × season × habitat), for example, resulted mainly because of the larger number of taxa caught in the plankton net in the beach habitat during summer (Fig. 4). The fewest taxa were caught by light traps during a full moon in autumn (Fig. 4). Overall, more taxa were caught during summer than in autumn, but the effect of moon phase depended on all the other major factors.

In the plankton net samples, the common taxa, except for the Retropinnidae, were more abundant in summer than in autumn (Fig. 5). Retropinnids were also more abundant in the light trap samples in autumn (Fig. 5). Two other taxa, unidentified Triptery-giidae and *Forsterygion varium*, were more abundant in the autumn light trap samples than in the summer samples.

Most of the common taxa were more abundant in the plankton net samples during a new moon than during a full moon (Fig. 5). The only exception to this was *Rhombosolea plebeia*, which was more abundant in the full moon samples. All taxa, with the exception of *Cologrammus flavescens*, were more abundant in the new moon light trap samples than in the full moon samples (Fig. 5).

The light traps and plankton net indicated very different abundance patterns between habitats for most common taxa. Most taxa, except *Sprattus* spp. and *Ruanoho decemdigitatus*, were more abundant in the plankton net samples from the beach habitat (Fig. 5). The light traps detected the opposite abundance patterns for most taxa; most of the common taxa, except Retropinnidae, were more common in the reef habitat (Fig. 5).

DISCUSSION

The taxonomic composition of larval fish in the samples was clearly dependent on the sampling method. The plankton net captured more taxa than the light traps, but many of these taxa were rare in the samples. All 12 taxa taken by the light traps were present in the plankton net samples. Although the light traps sampled a subset of the taxa captured by the plankton net, the relative abundance of individual taxa in the 2 methods was only weakly correlated.

Differences in the relative abundance of individual taxa between samples taken by the 2 methods were usually associated with differences in size-frequency

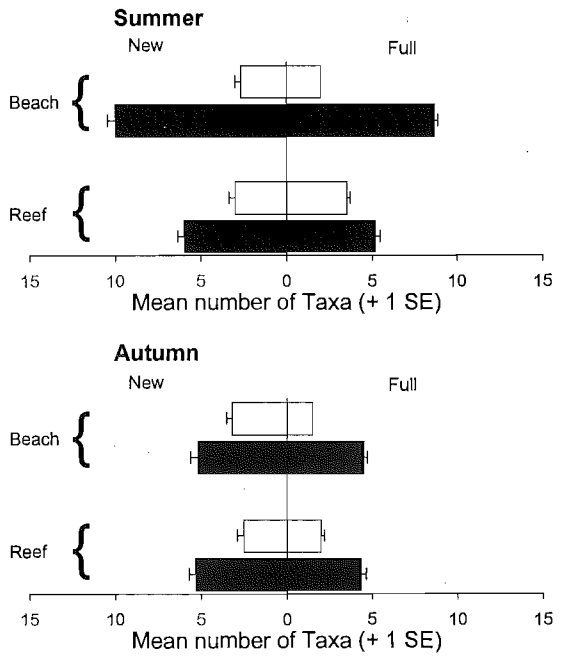

Fig. 4. Mean number of taxa (+1 SE) in samples collected in 2 seasons (summer and autumn) by 2 sampling methods (solid bars: plankton net; open bars: light trap) in 2 habitats (beach and reef) during 2 moon phases (new and full)

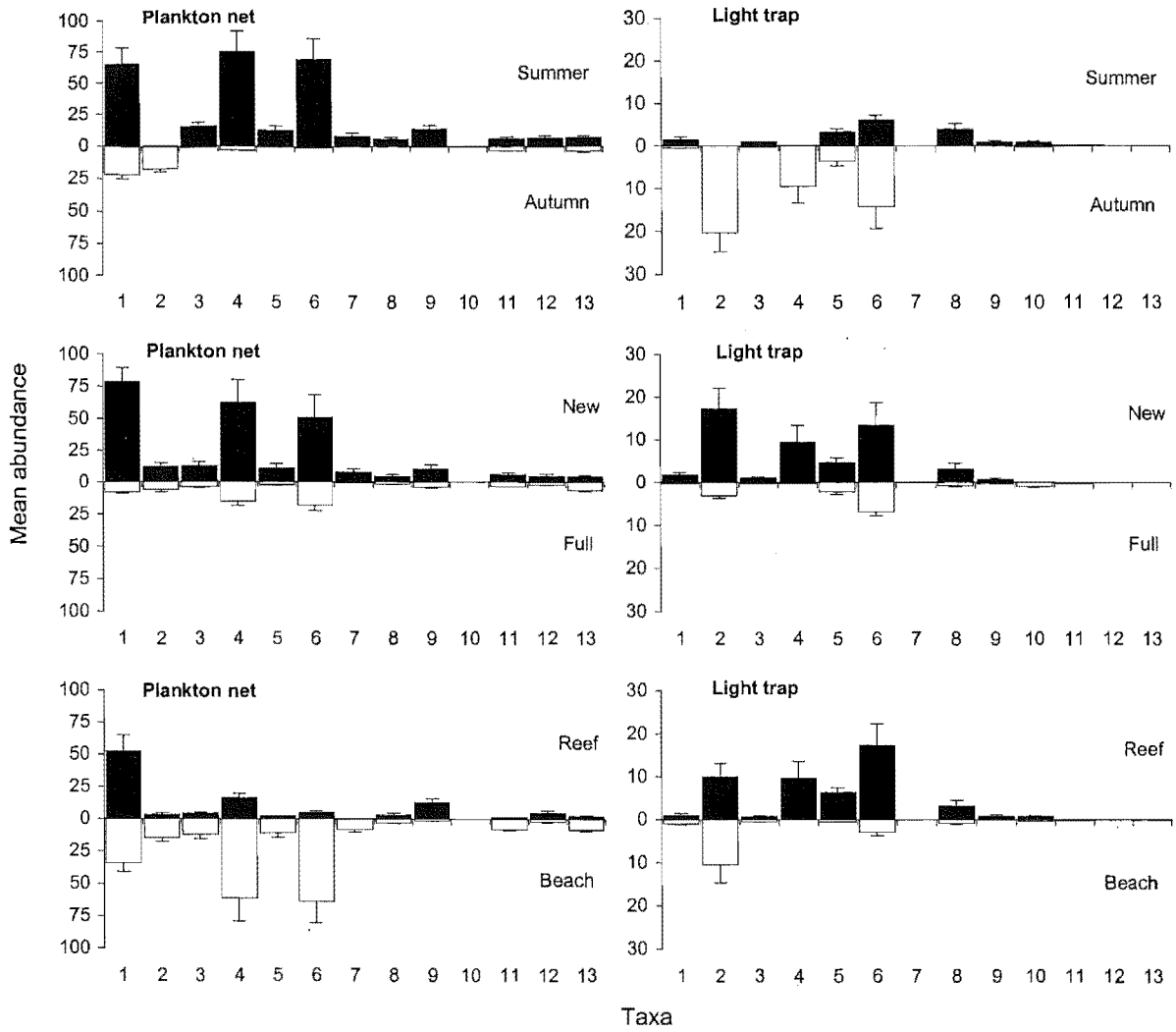

Fig. 5. Mean abundance (+SE) of taxa collected by plankton net and light trap during 2 seasons, 2 phases of the moon and in 2 habitats (1: *Sprattus* spp.; 2: unidentified Retropinnidae; 3: *Trachelochismus melobesia*; 4: unidentified Tripterygiidae; 5: *Forsterygion lapillum*; 6: *Forsterygion varium*; 7: *Gilloblennius tripennis*; 8: *Grahamina capito*; 9: *Ruanoho decemdigitatus*; 10: *Cologrammus flavescens*; 11: *Grahamichthys radiata*; 12: *Gobiopsis atrata*; 13: *Rhombosolea plebeia*)

distributions. The mean size of fish larvae in light trap samples was greater than that of plankton net samples for all of the common taxa. Of all the taxa, retropinnids had the most similar size distributions between methods. This is likely to be a consequence of the relatively large size of all retropinnid larvae sampled. By 20 mm SL retropinnid larvae are strong swimmers (Stephens 1983) and easily capable of reaching the light trap. Our results suggest that larger pelagic stages are more likely to be attracted to and swim into a light trap than are small stages, which is similar to the findings of Choat et al. (1993) in tropical waters. As a result of this selectivity, taxa that are only represented by small individuals in the plankton are less likely to occur in light trap samples unless they have a strong swimming ability, a strong positive phototactic response, or both.

In several cases, taxa that were abundant in the plankton net samples did not occur in the light trap samples (e.g. *Gilloblennius tripennis*, *Gobiopsis atrata* and *Rhombosolea plebeia*). This could be taken as evidence of these taxa not being positively phototactic. However, most of these fish were very small, and their absence from the light trap samples is likely to be a consequence of poor swimming ability. However, the light trap samples did contain very small individuals from 2 species of Gobiesocidae, suggesting that these species either possess a strong positive phototactic response during their early life, or are capable swimmers while still small, or a combination of both of these factors.

Samples taken by plankton nets also can be selective, both in terms of their taxonomic composition and size distribution. By actively filtering fish larvae from a water mass, plankton net characteristics, such as towing speed (Nakamura 1992), mesh size (Somerton & Kobayashi 1989) and mouth diameter (Thayer et al. 1983), interact with physical parameters such as light levels and water clarity (Brander & Thompson 1989), as well as the behavioural response of the fish larvae themselves (Leak & Houde 1987), to determine the composition and size structure of a sample. While small individuals may be under-represented in light trap samples, larger fish larvae are better able to avoid plankton nets (Brander & Thompson 1989) and consequently may be under-represented in plankton tows. Net avoidance is lessened at night, either through reduced visual avoidance, or reduced activity levels (Brander & Thompson 1989). Therefore, by using both methods at night, any differences in size distributions, due to net avoidance alone, should be decreased.

Little is known of the diel vertical distribution of larval fish in the study area. The vertical distribution of larval fish could affect the relative performance of the 2 sampling methods. It has been suggested that light traps may collect fish from the upper 5 m in tropical areas (P. J. Doherty unpubl., cited in Choat et al. 1993, Brogan 1994). This collection zone is likely to be less in our study area because of suspended matter in the water. However, our light traps appeared to illuminate the water within a radius of ca 3 m, were anchored 1 m below the surface and, therefore, were likely to have sampled fish from the upper 4 m (i.e. most of the water column at the 2 study sites). Conversely, the plankton net sampled a relatively narrow depth stratum, with the mouth fixed at a depth of 1 m. If any of the taxa present in the samples showed stratification in their vertical distribution, with a peak abundance outside the depth stratum sampled by the plankton net, it is likely that they would be under-represented in the samples. The extent of this bias between sampling methods is likely to vary with the depth of water at the sample site.

A major advantage of light traps over plankton nets is the ease with which light trap samples can be simultaneously replicated, by using multiple automated light traps. In deploying a plankton net, particularly in shallow rocky water with a small research boat, replicates can usually be obtained only by taking sequential tows. The time difference between replicate samples may result in increased inter-replicate variation. On most sampling occasions replicate light trap samples were less variable than the associated plankton tows. This reduced variance will make the light traps, when used in a structured design, more sensitive to detecting differences among treatment means.

Both sampling methods detected seasonal differences in the samples. Most taxa had a higher abundance in the summer samples. One exception to this was the retropinnids, which occurred almost exclusively in the autumn samples. Retropinnids are anadromous, with mature fish migrating during late summer and early autumn into freshwater to spawn (McDowall 1990). Consequently, retropinnid larvae are unlikely to appear in significant numbers in summer samples. The remaining taxa are predominately spring/early summer spawners (Ruck 1980, Ayling & Cox 1987, Paulin & Roberts 1992). The 2 sampling methods were generally in agreement with the patterns of seasonal abundance of individual taxa. Exceptions to this were unidentified Tripterygiidae, *Forsterygion lapillum* and *Forsterygion varium* which showed higher relative abundances in the autumn light trap samples. This may be a result of the size-selectivity of the light traps. During summer, tripterygiid larvae are common (as seen in the plankton net catch), but there are likely to be few large individuals for the light traps to attract. By autumn, the smaller individuals have grown to a size where they are more capable swimmers and more easily attracted to the light traps. These larger individuals may not appear in the plankton net samples because they are close to settlement and consequently are found close to the substrate. For each of the 3 tripterygiid taxa, the larvae caught by the light traps in autumn were larger than those caught by the plankton net in summer (K-S test, $p < 0.001$). However, there was no significant difference between the sizes of larvae caught by the light traps in summer and autumn.

Both sampling methods detected lunar differences in the samples. Most taxa had a higher abundance in samples collected during a new moon. While this pattern may be the result of a real difference in abundance between lunar phases, the efficiency of both sampling methods has been linked to light intensity. Avoidance of plankton nets is greater with increased light intensity (Thayer et al. 1983, Brander & Thompson 1989), and the catch of light traps has been found to be negatively correlated with moon illumination (Gregory & Powles 1985). Therefore, it would be expected that both sampling methods would capture fewer fish larvae during a full moon than during a new moon regardless of the relative abundance of the larvae during the different lunar phases.

The 2 sampling methods detected very different patterns of abundance between the 2 habitats. The light traps collected more of most taxa in the reef habitat, while the plankton net collected more in the beach habitat. An obvious reason for this discrepancy would be that smaller fish larvae were more abundant in the beach habitat and were captured by the plankton net,

while larger larvae were more abundant in the reef habitat and captured by the light traps. However, further analysis of the size structure of the samples taken by the 2 methods did not show this pattern. There are several other possible reasons for this discrepancy. Suspended matter, disturbed by wave action at the beach site, meant that the water clarity at the beach site was worse than at the reef site. This may have reduced the radius inside which fish could detect and be attracted to the light trap. Consequently, the light trap catches would be greater in the clearer water over the rocky reef. Another possible reason for the discrepancy in patterns detected by the 2 sampling methods is that there may have been a difference in water current speed at the 2 sites. Doherty (1987) identified this factor as being of paramount importance when comparing samples taken with light traps at fixed locations. *Sprattus* spp. and retropinnid larvae, which were generally larger than other taxa and consequently stronger swimmers, may have been less affected by current speed and thus showed relatively equal abundances in the 2 habitats.

Our study shares 4 families (Clupeidae, Gobiesocidae, Tripterygiidae and Gobiidae) with Brogan's (1994), 1 of the 2 other studies comparing light traps and plankton nets. Brogan recorded little overlap in the size distribution of clupeids caught by the 2 sampling methods. The 2 size distributions for tripterygiids broadly overlapped, but the modal size classes differed markedly. Brogan (1994) attributed much of this variation to fish larvae avoiding daytime tows with small nets. Such avoidance, particularly by larger and therefore faster swimming fish larvae, has been demonstrated in several other studies (Clutter & Anraku 1968, Barkley 1972, Suthers & Frank 1989). Both avoidance and diel vertical migration ensure that samples taken during daylight will not be equivalent to those taken at night (Leis 1991). In our study, both clupeid and individual tripterygiid species' size distributions overlapped broadly, but their means differed significantly. It is likely that by using both sampling methods at night the avoidance of plankton nets by larger fish was decreased.

Both previous studies comparing light traps and plankton nets in marine waters found that light traps collected fewer families than associated plankton tows. Brogan (1994) reported that his light traps collected 4 families that were not present in the plankton net samples. However, these families each accounted for a very small proportion (≤0.03%) of the total light trap catch. Neither our study nor Choat et al. (1993) recorded any families in light trap samples that were not present in plankton net samples.

Of the 19 large, inshore species whose adults were seen in extensive surveys of reefs around the Kaikoura Peninsula (Hickford & Schiel 1995), only 3 (*Scorpaena papillosus*, *Aldrichetta forsteri* and *Notolabrus celidotus*) were caught as larvae by either sampling method. These taxa were not abundant in the plankton samples collected. Larvae of *Latridopsis ciliaris*, *Notolabrus fucicola* and *Odax pullus* which, together with *Notolabrus celidotus*, dominate the inshore ichthyofauna were not found in our plankton samples. The reasons for the absence of these and other common species from the plankton samples are not clear, but probably involve a narrow depth distribution or extended offshore development. It is noteworthy that Kingsford & Choat (1989) found very few larvae of common reef-dwelling fish in their plankton net samples in northern New Zealand.

In summary, the light traps used in this study attracted and captured only a subset of the taxa caught by the plankton net. The relative abundance of individual taxa in the light trap samples was very different to that in the plankton net samples. For all commonly occurring taxa the light traps collected significantly larger fish larvae than the plankton net. The light traps were as capable as the plankton net in detecting interseasonal and lunar phase differences in the abundance of fish larvae. Water clarity and current speed should be equivalent between sites to use light traps for comparative studies. In this study, the light trap samples complemented those taken by the plankton net. While the plankton net captured more small fish larvae and individuals from rare taxa, the light traps captured more large larvae which may have avoided the plankton net. Rather than choosing between the 2 methods, both can be usefully combined in a sampling programme to provide more comprehensive insight into the ichthyoplankton spectrum associated with nearshore rocky reefs.

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